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Composition and variations in the occurrence of dissolved free simple organic compounds of an unproductive lake ecosystem in northern Sweden

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Abstract Low molecular weight organic carbon compounds are potentially important carbon and energy substrates to heterotrophic production in the aquatic environment. We studied the occurrence of dissolved free amino acids (AA), monosaccharides (CHO), and carboxylic acids (CA) in the subarctic Lake Diktar-Erik. The lake is unproductive with slightly humic water, and receives water via one major inlet stream draining a birch forest environment. The concentration of dissolved organic carbon (DOC) in the inlet stream was strongly correlated with the discharge. This relationship changed from season to season, indicating changes in the sources of the DOC entering the stream. AA and CHO each accounted for an average of less than 0.5% of the DOC. After high discharge events during the ice-free period, AA and CHO occurred in especially high concentrations. CA occurred in higher concentrations during the ice-free period, when it generally accounted for 20–30% of the DOC pool. The CA content relative to the total DOC pool was strongly inversely correlated with overall DOC concentration, and at low DOC levels the relative content of CA was high and vice versa. This followed a seasonal trend, with CA accounting for a smaller proportion of the DOC in winter and a larger part in spring/early summer. A conservative estimate suggested that the studied simple organic carbon compounds potentially could cover 30% of the bacterial gross production in the lake and therefore potentially also was an important source of CO_2 that occur in supersaturated concentrations in the lake.

Keywords Amino acids · Carboxylic acids · Carbohydrates · DOC · Respiration · Subarctic lakes

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Introduction

Lake ecosystems are affected in many ways by external input of various substances, and especially allochthonous input of organic matter has been found to affect the biota in the lakes (Steinberg 2003). The organic matter pool in northern boreal aquatic environments is dominated by humic substances, formed mainly during the degradation of terrestrially produced organic

matter and transported to the lakes in runoff (Heikkinen 1994 and references therein). Dissolved organic matter (DOM) in the aquatic environment comprises a range of substances, from simple compounds identifiable as various carbohydrates, carboxylic acids, phenols and tannins, amino acids, and hydrocarbons to more complex non-identifiable compounds comprised of hydrophilic acids and humic substances containing fulvic and humic acids (Thurman 1985). In lakes stained with organic matter, humic substances account for 50–90% of the DOC (Thurman 1985). Most humic substances in lakes originate from terrestrial sources, but a small part could form in the water itself through the condensation of smaller organic molecules (Steinberg 2003). A large part of the humic substances are recalcitrant and a lesser part of the DOC in humic lakes is available to aquatic biota (Tranvik 1988; Moran and Hodson 1990). Simple compounds such as amino acids and carbohydrates are more highly available than humic substances are, and serve as important substrates meeting bacterial carbon and nitrogen requirements in oligotrophic waters (Tranvik and Jørgensen 1995) and in more eutrophied lakes (Rosenstock and Simon 2001). The high bioavailability of simple organic compounds also makes these substances interesting from the perspective of carbon cycling in unproductive lakes, especially so in terms of what portion of the DOC pool that feed the heterotrophic bacteria, and thus also contributes to the production of CO_2 in lakes.

Unproductive lakes in the northern boreal region have been found to be net mineralization sites in the landscape and sources of CO_2 to the atmosphere (Jonsson et al. 2003; Sobek et al. 2003), and thus potentially important in the landscape carbon budget. We are therefore interested in assessing the role of simple organic carbon compounds as a potential important carbon source for CO_2 production in unproductive freshwater lakes. A literature search revealed surprisingly few studies of the distribution and occurrence of especially carboxylic acids, but also amino acids and carbohydrates in unproductive fresh waters.

Both amino acids and carbohydrates mostly occur in combined forms and to a lesser extent in free forms (Rosenstock and Simon 1993;

Tranvik and Jørgensen 1995; Volk et al. 1997). In general, dissolved free amino acids (AA) and dissolved free carbohydrates (CHO) account for at most a few percent of the DOC, and generally occur in concentrations less than 1 μmol l^{-1} (Gardner and Lee 1975; Jørgensen 1987; Lara et al. 1998). The CHO we have studied (monosaccharides) usually make up about 1% of the DOC pool in natural waters (Thurman 1985), but they still may dominate the dissolved CHO pool (Guéguen et al. 2006) in some systems. AA and CHO have a variety of sources, and, e.g. in streams, it has been found that terrestrial plants and soil organic matter make an important contribution, while in lakes both algal production and terrestrial input are important (Thurman 1985). Less is known of the distribution of dissolved carboxylic acids (CA). These acids are produced in the degradation of organic matter in soils and as root exudates (Fox and Comerford 1990; Tylor and Ström 1995). There are some indications that acetate may be the most dominant CA in fresh waters as it is formed as a key intermediate in oxidative degradation of organic matter by bacteria (Thurman 1985). Low molecular weight organic acids are also an important component of exudates from autochthonous production in the lakes (Sundh 1992). CA is also produced by photodegradation of DOM (Strome and Miller 1978; Allard et al. 1994; Bano et al. 1998; Lindell et al. 2000). CA produced via photodegradation of DOM has also been found enhancing bacterial growth (Bertilsson and Tranvik 1998). The CA typically produced by the photodegradation of DOM include acetic, formic, citric, and malonic acids (Wetzel et al. 1995; Bertilsson and Tranvik 1998). Still, the abundance and variation of especially CA's, but also AA's and CHO's, have not been thoroughly studied in unproductive fresh water systems that also are the most common fresh water system in northern boreal and subarctic regions.

The aims of this study are therefore to quantify the content and seasonal variations of dissolved free AA, CHO (the monosaccharides), and CA in the aquatic DOC pool of an unproductive northern lake ecosystem.

Materials and methods

Study site

Lake Diktar-Erik is situated approximately 15 km west of Abisko (18°49′ E, 68°21′ N) in northern Sweden. The lake is 8.8 ha in area, with a maximum depth of 17 m and a mean depth of 5 m. The theoretical water exchange time in the lake during the ice-free season 2003 (3 June until 17 October) was approximately 33 days. The lake is characterized as unproductive, with a total phosphorous concentration of approximately 6 µg l^{-1} and a total nitrogen concentration of approximately 200 µg l^{-1} (Karlsson et al. 2002). The average chlorophyll a concentration during the ice-free season of 2003 was approximately 0.4 µg l^{-1} (range: 0.2–0.7 µg l^{-1} Jonsson, A., unpubl.). The water is brown coloured from DOC, and the DOC concentration usually varies between 3 and 10 mg l^{-1}. The lake has one major inlet stream, which drains approximately 94% of the catchment, and one outlet. The catchment is 544 ha and consists of bare rock outcrops and boulder landscape (49% of catchment area), subalpine birch forest (28%), alpine heath (10%), mires (7%), and water (5%). The average annual air temperature at the site is approximately –1°C.

Sampling

Water samples for DOC, AA, CHO and CA were taken from the inlet stream, lake, and outlet stream between December 2002 and January 2004. In winter (October–April), water samples were taken once a month from the inlet and the lake. From spring until autumn (May–September), water samples were taken approximately once a week from the inlet, lake, and outlet. Inlet and outlet samples, and samples from below the lake ice, were taken with a Ruttner sampler. In winter, lake samples were taken 1 m below the ice surface. During the ice-free season, composite samples were taken from the lake using a Ramberg sampler (plastic tube sampler, 2 m long and approximately 2 l volume). These samples were taken at five different sampling locations in the lake and pooled to make one composite sample

representing the whole lake volume. At each of these five locations water were taken at 2-m intervals from the surface to the bottom; the sampling volume of water in each 2-m layer was calculated using a depth–volume relationship determined from echo-sounding the lake (Karlsson et al. 2001). On 6 August a depth gradient in a central point in the lake was sampled using a Ruttner sampler. Samples were taken at 1 m, 4 m, 8 m and 15 m water depths.

Water samples used for DOC analysis were filtered using pre-ignited (500°C for 3 h) filters (Whatman GF/F) and acidified with 100 µl 10% HCl 10 ml^{-1} of sample water. Another 20 ml of water was also filtered into glass vials for the analyses of CA, AA, and CHO. During transport from the lake to the laboratory, water samples were stored in a cooling box; on arrival at the laboratory, approximately 2 h after sampling, the samples were immediately frozen to await analysis. Prior to the analyses of CA, AA, and CHO, the thawed water was filtered through Acrodisc PF 0.8/0.2 µm filters pre-rinsed with 30 ml of distilled water.

Pressure transducers were installed between 6 June and 14 October in the inlet and between 21 May and 14 October in the outlet. These were connected to data loggers, which registered the water level every 10 min. Manual water level measurements were made in early spring prior to mounting the data loggers. Water level and discharge relationships had earlier been determined (Åberg et al. 2005), and were used to calculate the discharge.

Analyses

DOC samples were analyzed using a Shimadzu 5000-TOC. Analyses of CA, AA, and CHO (the monosaccharides) were conducted using a high pressure liquid chromatography (HPLC) system from Dionex, especially equipped to meet the analysis requirements of each of the three compound groups. Analysis of CA was performed using suppressed conductivity detection (AMMS-ICE II) and the IonPac ICE-AS6 analytical column. Degassed 0.4 mM Heptafluorobutyric acid was used as the eluent with a flow rate of 1.0 ml min^{-1}. The injection volume was 50 µl. For

additional details see Dionex (2002a). Analyses of AA and CHO were performed using electrochemical detection with a gold amperometry cell and the AminoPac PA10 (AA) and CarboPac PA20 (CHO) analytical columns. The injection volume was 25 µl. For AA analysis a degassed gradient mixed of 0.25 M NaOH and 1.0 M Na-acetate was used to elute the sample, followed by a clean-up step of 100% 0.1 M HAc, with a flow rate of 0.25 ml min^{-1}. For additional details see Dionex (2003). For CHO analysis the eluent was generated by a EGC II KOH cartridge (Dionex 2004), with a flow rate of 0.10 ml min^{-1}. For additional details see Dionex (2002b). The HPLC set up and chromatograms were handled using chromelion 6.5 chromatography management system (Dionex). The retention times of the compounds were obtained from chromatograms of mixed standard solutions of the compounds within each element group. In less apparent cases the identity of compounds was secured by standard addition of either compound to the sample. The concentration of a compound was obtained by comparison of the peak area of the compounds to a calibration curve, which was run for each compound in the concentration range of the samples using a minimum of 4 concentrations. The minimum concentration of a compound that could be adequately detected (detection limit) was taken as the compound concentrations that provided a signal to noise ratio of two (Snyder and Kirkland 1979). When the signal to noise ratio varied between the compounds within an element group the highest concentration that provided a ratio of two was chosen as detection limit. The detection limit were for CA 1.0 µM, AA 0.02 µM and CHO 0.02 µM.

Statistical tests

Differences between groups were tested using a t-test or a rank sum test, with a significance level of 0.05 (Sigmastat 3.0, SPSS). Data for correlations were tested for normality and if necessary transformed. Regressions between DOC concentration and discharge were made by testing different average discharge times to obtain the most significant results.

Calculations

The relative importance of simple organic carbon compounds as a carbon source for the bacterial gross production (BGP) during the ice-free period was calculated by dividing an estimated biotic consumption of simple organic compounds with an estimated BGP. The heterotrophic BGP during the studied ice-free season was estimated using the measured average net bacterial production (2.1 µg C l^{-1} d^{-1}) in the lake during the ice-free season of 1999 (Karlsson et al. 2001), by applying bacterial growth efficiencies (BGE) of 0.1, 0.2 or 0.3. The biotic consumption (assumed to be only by heterotrophic bacteria) of analysed simple organic compounds in the lake was calculated by a simple mass balance calculation. This was done by multiplying the difference in median concentration (Table 1) between the lake and the outlet with the average daily discharge during the ice-free period. Since AA had a higher concentration

Table 1 The median (M) DOC concentration (mg C l^{-1}) and the median (±SD) carbon content (µg C l^{-1}) found in dissolved free amino acids (AA), monosaccharides (CHO), and carboxylic acids (CA) in the different compartments (number of samples) during the ice-free season

	DOC	AA		CHO		CA	
	M	M	% DOC	M	% DOC	M	% DOC
Inlet (14)	5.4	13 (32)	0.5	11 (29)	0.2	1211 (223)	22
Lake (10)	4.2	13 (296)	0.3	17 (160)	0.4	1265 (193)	31
Outlet (15)*	4.8	25 (155)	0.5	2.5 (70)	0.1	1074 (205)	18

Also included is the median percentage of each component of the total DOC concentration (% DOC)

* For CA's 14 samples, data from 11 July not included

in the outlet than in the lake, AA was not included in the calculation.

Results

DOC concentrations

DOC concentrations changed markedly from season to season, and the pattern was similar in the inlet, outlet, and lake (Fig. 1). In general, concentrations were highest during the winter low flow and autumn high flow, and lowest in early summer after the high discharge arising from the snowmelt. The greatest seasonal changes were observed in the inlet water. During the ice-free period the DOC concentration in the inlet water was almost twice as high (average 6.3 mg l⁻¹) in the late summer/autumn period as the concentration in early summer (average 3.9 mg l⁻¹) (Fig. 1). The DOC concentration was strongly correlated with discharge in the inlet in these two periods, but the relationship changed: in early summer, the DOC concentration in the inlet was strongly positively correlated with the daily mean discharge ($r^2 = 0.86$, $F = 25$, $P = 0.007$, $n = 6$); but in late summer/autumn, the DOC concentration was strongly positively correlated with the 12-d average discharge ($r^2 = 0.91$, $F = 70$, $P < 0.001$,

$n = 9$). These relationships had similar slopes (t-test, $P = 0.218$), but their intercepts differed (t-test, $P < 0.001$). During the very high discharge in spring (Fig. 1), there was no relationship between discharge and the DOC concentration.

Concentrations of specific DOC entities

The median AA and CHO contents were less than 1% of the DOC (Table 1), and most of the simple compounds were made up of CA, which amounted to between approximately 20% and 30% of the DOC pool (Table 1). Thus, unidentified components comprised 71% to 78% of the DOC pool in the system. This pool was assumed to consist mainly of humic substances and is referred to as such hereafter. This assumption was also strengthened by that the water in Lake Diktar-Erik was highly brown coloured and had a absorption (250 nm) per DOC ratio that was approximately 6 times higher than in alpine clear water lakes in the area (see Jonsson et al. 2003, where Lake Diktar-Erik is no. 5 in Tables 1 and 2). The unidentified pool, however, probably also included unidentified simple compounds, such as hydrocarbons, polysaccharides and phenols, which however do not make up any larger part of the DOC in low productive waters (McDowell and Likens 1988).

AA occurred in higher concentrations after high flow situations in spring and in autumn (Fig. 2). Tyrosine (Tyr) was the most common AA, while others occurred in very low concentrations (Table 2). Alanine (Ala), glycine (Gly), and serine (Ser) were other free amino acids also found in several samples. Gly and Ser were found in high concentrations on a few occasions in the inlet and in the outlet. Ala occurred in a very high concentration on one occasion in the lake. Other free amino acids found were aspartic acid (Asp), glutamic acid (Glu), leucine (Leu), lysine (Lys), methionine (Met), phenylalanine (Phe), proline (Pro), threonine (Thr), and valine (Val), but these were generally found in concentrations less than 0.1μg C l⁻¹. The free amino acids arginine (Arg), isoleucine (Ile), histidine (His), glutamine (Gln) asparaginine (Asn),cystine (Cys), and tryptophan (Try) were also detectable by HPLC, but were not present in the samples.
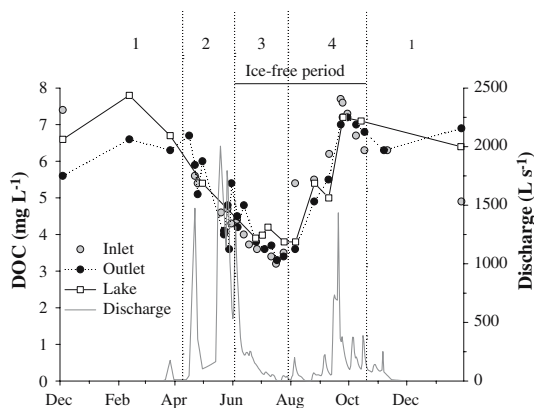

Fig. 1 The DOC concentration in the different compartments of Lake Diktar-Erik during the sampling period. Also shown is the discharge. Numbers 1–4 represent the study periods; 1 equals the winter period, 2 the spring period, 3 the early summer period and 4 the late summer/autumn period

Table 2 The median (M) (±SD) carbon content (μg C l^{-1}) of the most abundant dissolved free carboxylic acids (CA), amino acids (AA), and monosaccharides (CHO) substances during the ice-free season in the different compartments (number of samples)

Component	Substance	Inlet (14)		Lake (10)		Outlet (15)*	
		M	% TC	M	% TC	M	% TC
CA	Glycolate	852 (176)	72	991 (219)	77	754 (183)	78
	Citrate	179 (84)	16	197 (93)	18	122 (74)	11
	Formate	49 (46)	3	25 (41)	2	51 (51)	4
	Acetate	31 (27)	2	16 (40)	1	13 (73)	1
AA	Tyr	9.3 (9.1)	62	8.7 (11)	69	24 (13)	76
	Ser	1.4 (13)	12	2.5 (16)	10	1.8 (32)	10
	Ala	1.7 (8.0)	13	1.1 (237)	8	1.0 (15)	3
	Gly	0.0 (9.8)	0	1.0 (31.1)	7	0.0 (75.6)	0
CHO	Glucose	5.1 (5.2)	59	5.3 (39)	50	2.5 (17)	62
	Fructose	4.8 (24)	41	10 (121)	50	0.0 (47)	36

Also included is the median percentage of the total component (% TC)

* For CA 14 samples, data from 11 July not included

The concentration of the studied CHO was high in connection to the spring and autumn discharge peaks (Fig. 3). Glucose and fructose dominated the CHO pool (Table 2), which was nevertheless mostly below the detection limit in the outlet water in summer. Arabinose was found in a few samples, especially from the outlet; mannitol, fucose, rhamnose, galactose, mannose, xylose, and ribose were also detectable by HPLC but not present in the samples.

The total CA concentration varied from season to season, with low concentrations in winter and high ones in summer/autumn (Fig. 4). Glycolate was the most abundant of the analyzed carboxylic acids, followed by citrate, while others occurred in markedly lower concentrations (Table 2). When discharge increased during the snowmelt, CA concentrations also increased, the increase mainly being due to increases in the citrate, glycolate, and formate concentrations. The formate concentration increased markedly starting from the beginning of July. CA concentrations decreased during the high discharge in autumn, mainly due to decreases in citrate and glycolate concentrations. The sampled depth gradient in August in the lake indicated that the two most common carboxylic acids, citrate and glycolate, behaved somewhat differently. Citrate occurred at a higher concentration in the surface water, while glycolate occurred uniformly throughout most of the water column (Fig. 5). The occurrence of
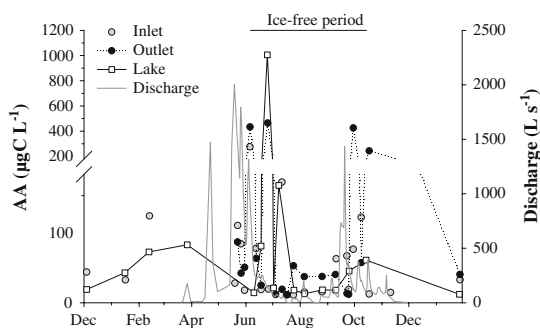
Fig. 2 The content of dissolved free amino acids (AA) in Lake Diktar-Erik. Also shown is the discharge. Note the break of the y-axis for the AA concentration
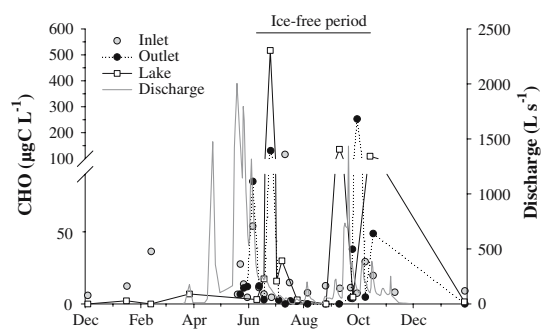
Fig. 3 The content of dissolved free monosaccharides (CHO) in Lake Diktar-Erik. Also shown is the discharge. Note the break of the y-axis for the CHO concentration
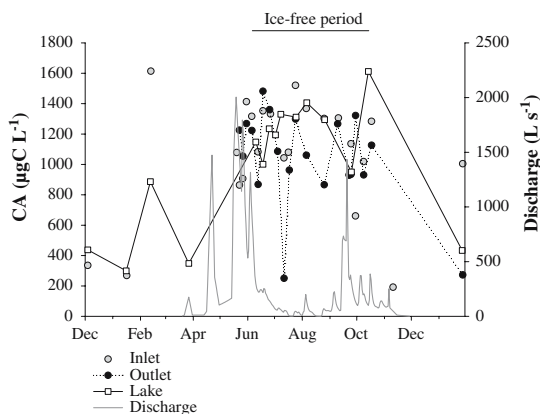
Fig. 4 The content of dissolved free carboxylic acids (CA) in Lake Diktar-Erik. Also shown is the discharge. The low value found in the outlet in the middle of July was considered as an outlier, which is included since no analytical error could be found

Fig. 6 Relative dissolved free carboxylic acid (CA) content of as a proportion of the total DOC pool, plotted against the DOC content. All data from the inlet, outlet, and lake have been used ($n = 54$). The relationship can be described by the following function: CA% = 79.7 – 25.0 × sqrt [DOC], $r^2 = 0.72$, $F = 131$, $P < 0.001$. The star represents a value from the outlet (11 July), which was considered as an outlier and not included in the analysis (see Fig. 4)

tartrate, lactate, and acetate displayed no clear seasonal pattern. Tartrate and lactate were typically found in concentrations less than 0.1 µg C l^{-1}. The relative CA content also increased as the DOC concentration decreased; this indicated seasonal variation in the relative CA content, with a higher proportion evident in spring/early summer (Fig. 6). The carboxylic acids malate, aconitate, and succinate were also detectable by HPLC but not present in the samples.
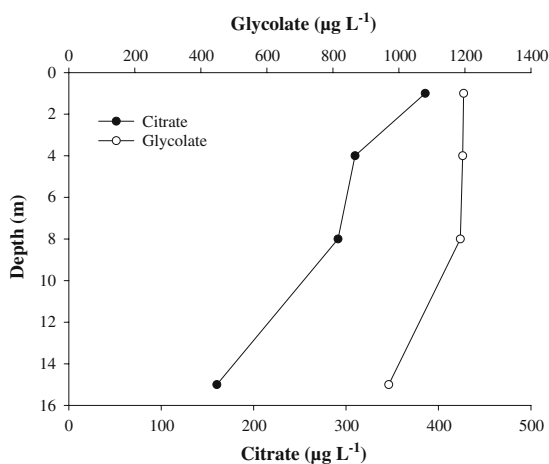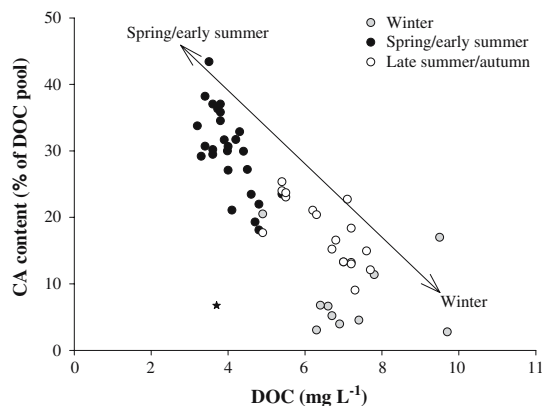

Fig. 5 The distribution of citrate and glycolate throughout the water column of the lake. Samples were taken on 6 August

Estimated BGP in the lake during the ice-free season varied between 36 and 107 mg C m^{-2} d^{-1} depending on the BGE used. From the mass balance calculation we estimated the biotic consumption of CHO and CA to 32 mg C m^{-2} d^{-1}, and thus these components could potentially cover between 30 and 89% of the BGP (Table 3) depending on the actual BGE.

Discussion

The decreasing DOC concentration observed during the spring high flow (Fig. 1) differs from the often-observed phenomenon of increasing DOC content of stream waters during snowmelt (Bishop and Petterson 1996), but corresponds with what Laudon et al. (2004) found in wetland dominated catchments. The Diktar-Erik catchment is, however, not wetland dominated and only 7% of its area consists of mires. Thus, the large decrease of the DOC concentration to the period previous to the snowmelt was possibly because of the depletion of the mobile DOC pool in the soils, due to the flushing of a very large amount of water through the soil horizons, as has been previously demonstrated by Hornberger

Table 3 Estimated bacterial gross production (BGP), expressed both as volumetric and area based numbers, using different bacterial growth efficiencies (BGE), the estimated biotic consumption of dissolved free monosaccharides (CHO) and carboxylic acids (CA) calculated in the mass balance calculation, and the percentage of BGP that is covered by the biotic consumption of CHO and CA

BGE	Bacterial gross production		Biotic consumption of CHO and CA	BGP covered by CHO and CA
	μg C l^{-1} d^{-1}	mg C m^{-2} d^{-1}	mg C m^{-2} d^{-1}	(%)
0.1	21.0	107		30
0.2	10.5	53	32	59
0.3	7.0	36		89

et al. (1994) in the Snake River, Colorado, USA. A large part of the catchment (49%) also lacks a soil cover, which limits the terrestrial pool of available DOC.

In summer we observed significant positive relationships between DOC and discharge in the inlet, indicating that more DOC flushes out from the soils with increasing discharge. Concentrations were, however, lower in early summer (Fig. 1). The significantly lower intercept in the relationship using data from the early summer period compared to later periods was probably an effect of the large flush and depletion of the mobile soil DOC pool in the previous snowmelt period.

The higher intercept in the DOC discharge relationship and higher DOC concentrations found in late summer/autumn could possibly be attributed to an increased production of organic material in the catchment soils during summer. Corresponding observations were made by Yano et al. (2004), who studied seasonal changes in the release of DOC from temperate forest soils and found a larger release after the summer. They speculated that this was due to an accumulation of DOC in the dry summer months or to a higher root production of DOC in autumn. Aitkenhead et al. (1999) also found a strong correlation between the soil organic carbon pool and the DOC content of streams in small ($<$5 km^2) catchments. In light of these findings, our finding of higher DOC concentrations in the late summer/autumn period (Fig. 1) likely stems from changes in the soil DOC pool or in the release of DOC from this pool.

Although the DOC content increased in the autumn, the CA content remained relatively stable over the entire ice-free season (Fig. 4). This is in line with the findings of several studies of podzol soils, which have found little variation in CA content over the entire unfrozen season (van Hees et al. 2000; Kryszowska et al. 1996). However, our data suggests a strong negative relationship between the *relative* content of CA in the DOC pool and the DOC concentration (Fig. 6), indicating that the input of humic substances changes while the CA input remains fairly stable. The observed negative relationship indicates a time-line, since the higher concentrations of DOC and the lower proportion of CA were found later in the season. The DOC transported in the late summer/autumn period therefore contained more humic substances than during the early summer period.

In winter the production of CA seemed to be much lower than during the rest of the year since water draining into the system during winter contained 2 to 3 times less CA. However the DOC concentration was high, indicating a very high content of humic substances in the DOC draining in to the system. We surmise that these observations could possibly stem from processes in the terrestrial system from which the DOC likely emanates.

Compared to its level in soil waters, the CA content of the stream and lake waters was low (van Hees et al. 2000, 2005). However, the proportion of CA in the DOC pool was high, generally ranging from 20% to 30% of the DOC pool (Table 1). Thurman (1985) stated that

between 5% and 8% of the DOC should generally be CA in aquatic systems. Lake Diktar-Erik thus had a significantly higher relative content of CA, which could indicate that the properties of the studied soil–water system differ from those of other systems. Or since CA has seldom been analyzed or properly studied, the sharply divergent findings might simply reflect our current lack of knowledge of CA in lake water.

The major components of the CA pool, glycolate and citrate (Table 2), are formed in metabolic processes in plants and animals (Thurman 1985). Planktonic production and respiration was severely nutrient limited in the studied system, and production was very low (Karlsson et al. 2002). Therefore, other processes than plankton production must have been responsible for the high concentrations in the water. Photodegradation is a process known to produce CA in aquatic systems (Bertilsson and Tranvik 1998)—mostly acetate, formate, and citrate (Wetzel et al. 1995). There was however no strong indication that photodegradation in the water was an important production process of CA in the lake, since the concentration did not differ between the inlet and the lake (Tables 1 and 2). In the depth gradient taken at the beginning of August (Fig. 5), the concentration of glycolate was rather stable throughout the water depth, which should not be the case if it were produced at a high rate in the surface water. In contrast, citrate was found in higher concentrations in the surface water (Fig. 5), indicating possible photoproduction in the surface water. However, the most plausible explanation is that the main source of CA in the aquatic environment of Diktar-Erik is export from terrestrial sources.

The simple compounds are potentially important for bacterial production in lakes (Azam and Hodson 1977). AA and CHO are most likely to be consumed, and consequently occurred in low concentrations. The studied CHO were practically absent from the outlet in summer (Fig. 3) indicating an uptake by biota in the water. Interestingly, there seem to be high concentrations of AA and the studied CHO in connection with the high water flow situations (Figs. 2, 3) that at least during short term would benefit heterotrophic bacteria in the system. Bacterial activity

has also been found to increase during high-flow situations in unproductive boreal waters (Bergström and Jansson 2000). An increased bioavailability of the dissolved organic matter was also seen in connection to spring high flow in two small oligotrophic boreal forest streams in northern Sweden (Stepanauskas et al. 2000).

CA occurs in high concentrations and serves as an abundant carbon source for heterotrophic bacteria. Several studies have demonstrated a high utilization of CA by bacteria in lake waters (Robinson et al. 1973; Bertilsson and Tranvik 1998; Wetzel et al. 1995). The CA pool was dominated by glycolate (Table 2); several studies have found that the glycolate pool in aquatic systems is turned over more slowly than are other carboxylic acids and other simple organic compounds (Robinson et al. 1973; Wright 1975). Wright (1975) found that glycolate is mainly used by aquatic bacteria as an energy source rather than as a building block, and concluded that the heterotrophic potential of glycolate is comparable to that of other commonly utilized substrates given enough time. Simple compounds, which in the lake appeared to be largely of allochthonous origin, could therefore play an important role in the growth of plankton in the lake.

The concentration of simple organic compounds was also high enough to satisfy a large part of the heterotrophic bacterial gross production (Table 3). The estimates given in Table 3 must be considered as conservative since there also should be a consumption of AA, which was not included in the estimates since the concentration was higher in the outlet than in the lake. Also, there should be a constant turnover of these simple organic compounds, since they have a very short turnover time—in the order of hours, that is not seen using a mass balance approach.

Åberg et al. (2005) estimated the emission of CO_2 from the lake in ice-free season of 2003 to 113 g C m^{-2} d^{-1}, this number is close to the calculated BGP using an BGE of 0.1 (Table 3). Åberg et al. (2005) also found that the production of CO_2 within the lake was the main source of emitted CO_2. This implies that the BGE should be close to 0.1 and that potentially the dissolved free simple organic compounds contributed to 30% of the estimated BGP in the lake, and it also

indicated these compounds potential role as substrates for the in-lake CO_2 production in Lake Diktar-Erik. These estimates should however be taken with care since the difference in concentration between the lake and the outlet of CA (Table 1) was significant only at $P < 0.10$ ($P \leq 0.082$), and there was no significant difference in CHO. As discussed above, the low concentration of CHO in the outlet (below detection) during most part of the mid-summer (Fig. 3) does indicate a biotic consumption. Based on these facts we do consider our estimate of the biotic consumption (calculated to 32 mg C m^{-2} d^{-1}) of CHO and CA to be realistic.

Carbon uptake by heterotrophic bacteria is also transferred to higher trophic levels, such as the crustacean zooplankton. Karlsson et al. (2003) found that more than 60% of the zooplankton biomass in Lake Diktar-Erik consisted of carbon of allochthonous origin, as a result of bacterial utilization of allochthonous material and the transfer of carbon via grazing up to the crustaceans. We can thus conclude that dissolved free simple organic compounds are potentially important for heterotrophic bacterial growth and respiration, and also for the emission of CO_2 as well as energy transfer to higher trophic levels.

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