Bacterial use of allochthonous organic carbon for respiration and growth in boreal freshwater systems

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Aquatic systems worldwide receive large amounts of organic carbon from terrestrial sources. This ‘allochthonous’ organic carbon (AlloOC) affects critical physical and chemical properties of freshwater ecosystems, with consequences for food web structures and exchange of greenhouse gases with the atmosphere. In the boreal region, loadings of AlloOC are particularly high due to leaching from huge organic deposits in boreal forest, mire and tundra soils.

A main process of AlloOC turnover in aquatic systems is its use by heterotrophic bacteria. Applying a bioassay approach, I measured the respiration and growth (production) of bacteria in northern Sweden, in streams and lakes almost totally dominated by AlloOC. The objective was to elucidate how variations in AlloOC source, age, composition and concentration impact on its use by aquatic bacteria, and how AlloOC properties, in turn, are regulated by landscape composition and by hydrology.

The bacterial respiration (30-309 µg C L⁻¹ d⁻¹) was roughly proportional to the concentration of AlloOC (7-47 mg C L⁻¹), but not significantly related to AlloOC source or character. Bacterial production (4-94 µg C L⁻¹ d⁻¹), on the other hand, was coupled to the AlloOC character, rather than concentration. A strong coupling to AlloOC character was also found for bacterial growth efficiency (0.06-0.51), i.e. production per unit of assimilated carbon. Bacterial production and growth efficiency increased with rising concentrations of low molecular weight AlloOC (carboxylic acids, free amino acids and simple carbohydrates). While the total AlloOC concentrations generally were the highest in mire-dominated catchments, low molecular weight AlloOC concentrations were much higher in forested catchments, compared to mire-dominated. These patterns were reflected in a strong landscape control of aquatic bacterial metabolism. Moreover, high flow episodes increased the export of organic carbon from forests, in relation to the export from mires, stimulating the bacterial production and growth efficiency in streams with mixed (forest and mire) catchments. The potential of AlloOC to support efficient bacterial growth decreased on time-scales of weeks to months, as the AlloOC was aged in laboratory or lake in situ conditions.

To conclude, landscape, hydrology and conditions which determine AlloOC age have large influence on bacterial metabolism in boreal aquatic systems. Considering the role of bacteria in heterotrophic food chains, these factors can have spin-off effects on the structure and function of boreal aquatic ecosystems.

Keywords: lakes, streams, boreal, bacterial respiration, bacterial production, bacterial growth efficiency, allochthonous organic carbon, low molecular weight compounds
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**List of papers**

The thesis is based on the following papers, which will be referred to in the text by their Roman numerals:


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Introduction

Aquatic systems of the world annually receive 1.9-2.7 billions ($10^9$) of tonnes of allochthonous carbon, i.e., carbon from terrestrial sources (Cole et al. 2007; Battin et al. 2009). An important component of this flux is leaching of organic carbon from soils to streams. The allochthonous organic carbon (AlloOC) is a diverse mix of root exudates, microbial metabolites and decaying plant material and organism remains. For a long time, freshwater systems were considered a passive pipeline, transporting AlloOC to the oceans. Today, there is increased recognition of the AlloOC interactivity, fundamentally affecting physical, chemical and biological properties of lake and river ecosystems (Findlay and Sinsabaugh 2003). AlloOC is involved in light extinction (Karlsson et al. 2009), natural acidity (Kortelainen 1999) and organic matter flocculation (Von Wachenfeldt 2008). It adsorbs metals, pollutants (Tipping 1993) and nutrients (Jones et al. 1993). Moreover, various allochthonous compounds can be metabolized by microorganisms, primarily heterotrophic bacteria (Tranvik 1988; Del Giorgio et al. 1997; Jonsson et al. 2001), with spinoff effects on lake food-web structures (Jansson et al. 2007) and the landscape exchange of greenhouse gases with the atmosphere (Algesten et al. 2004; Cole et al. 2007).

Aquatic bacteria use AlloOC for two major purposes: respiration and growth. Bacterial respiration (BR) is a process whereby energy is obtained, typically in a series of redox reactions, where reduced carbon atoms donate electrons to oxygen ($O_2$) under formation of carbon dioxide ($CO_2$) (Del Giorgio and Williams 2005). Respiration of AlloOC represents a return to the atmosphere of $CO_2$ previously fixed in terrestrial systems (Cole et al. 1994) and may constitute an important component in landscape carbon balances (Cole et al. 2007; Battin et al. 2009). Growth, or bacterial production (BP), is a process in which organic carbon is transformed and incorporated into bacterial biomass. In systems of extremely low primary production, e.g., due to light extinction (Karlsson et al. 2009), BP based on AlloOC is an important alternative point of entry for energy in aquatic food webs (Jansson et al. 2007). Protozoans (Isaksson et al. 1999; Bergström 2009), but sometimes also metazoans (Pace et al. 1990), are effective grazers of bacteria, often assimilating a major portion of the BP. Another related metabolic measure of importance is bacterial growth efficiency (BGE), defined as BP divided by the sum of BR and BP (Del Giorgio and Cole 1998). BGE states the degree to which the metabolized carbon supports BP (and not BR), which makes the carbon potentially available to higher levels of trophy.

Boreal forest and tundra ecosystems hold one of the largest pools of organic carbon on the surface of the earth (Apps et al. 1993; Jobbagy and Jackson 2000; Tarnocai et al. 2009). The possibility that natural organic deposits could become sources of greenhouse gases by influence of climate change (Friedlingstein et al. 2006; Solomon et al. 2007) has drawn increased attention to carbon cycling in boreal ecosystems, including the aquatic components and fluxes through bacteria. While the current size of boreal aquatic carbon fluxes is beginning to be understood (Algesten et al. 2004; Roehm et al. 2009b), there is vague knowledge on the regulation of the basic metabolic processes in which
bacteria use AlloOC. Very few boreal studies have been conducted on how BR, BP and BGE relate to the source, age and molecular composition of AlloOC and how these factors, in turn, may be regulated by hydrological processes that govern the export of AlloOC from soils to streams and lakes. Thus, research is strongly needed to be able to predict how boreal aquatic bacterial communities will respond to possible future environmental changes, e.g., in land use or climate, which affect hydrology and AlloOC loadings.

The two major sources of AlloOC in boreal freshwaters are coniferous forests and Sphagnum-dominated peat wetlands, i.e., mires (Ågren et al. 2007). Forests and mires differ markedly in their organic carbon export dynamics. Most of the AlloOC from forest ecosystems originates in superficial soil layers (Laudon et al. 2004; Sanderman et al. 2009). This carbon is generated via degradation of detritus (e.g., spruce needles), but also through leaching of low molecular weight (LMW) photosynthates from mycorrhizal plant roots (Högberg et al. 2001; Giesler et al. 2007). High organic carbon export rates and high export of young potentially bioavailable compounds take place when the forest soil water table is high and the superficial soil layers are hydrologically active (Buffam et al. 2001; Sanderman et al. 2009). Contrary, the organic carbon leaching from mires, which are constantly saturated with water, show little temporal variations in quality (Ågren et al. 2008b) and constitutes mainly of bryophytic material known to be slow-degrading. For example, Sphagnum litter has low nutrient contents (Asada and Warner 2005) and comprises recalcitrant carbon compounds (Johnson and Damman 1991) as well as chemical species with antimicrobial properties (Verhoeven and Toth 1995; Verhoeven and Liefveld 1997). Despite these fundamental differences between mire-dominated and forested systems, the influence of the landscape composition on bacterial metabolic processes in receiving freshwaters has rarely been addressed.

Hydrology is a key for understanding of AlloOC loadings in boreal aquatic systems. Hydrological processes determine the water flux, the water concentration of AlloOC (Laudon et al. 2004) and the AlloOC source and character (Sanderman et al. 2009). It has been hypothesized that with rising discharge, an increasing share of the AlloOC pool in streams can support bacterial metabolism because of higher contents of bioavailable compounds from superficial forest soils. However, despite its theoretical basis, this hypothesis has received little empirical support (Leff and Meyer 1991; Volk et al. 1997; Buffam et al. 2001). Another possibility, not previously tested, is that variability in AlloOC bioavailability is caused by interactions between discharge and landscape composition. Mires often contributes with the major share of total landscape export of organic carbon in low flow conditions (Schiff et al. 1998; Creed et al. 2003), but forests can contribute with the major share during high flow (Laudon et al. 2004; Buffam et al. 2008). Thus, the most pronounced coupling between hydrology and AlloOC bioavailability may not be found in streams with 100% forested catchments, but in ‘mixed’ streams that alternate between pre-dominantly receiving AlloOC from the two very different sources forests and mires.
AlloOC comprises a continuum of components that are available to bacteria on different timescales and for consumption with different BGE. Dark bioassays have shown that, provided essential nutrients are available, i.e., inorganic phosphorus (P) and nitrogen (N), ca 10% of AlloOC can be used by bacteria within weeks at high rates and with high BGE (Moran and Hodson 1990; Tranvik 1998; Lennon and Pfaff 2005). Additionally ca 50% can be consumed on the time scale of years at lower rates and with lower BGE (Raymond and Bauer 2001; Eiler et al. 2003). Thus, it is possible to hypothesize that support for bacterial metabolism by AlloOC decreases as the organic carbon ages with its residence time in natural aquatic systems. Increased rates of BP and BR per unit of available AlloOC have been observed several times during high flow episodes in boreal lakes and estuaries (Wikner et al. 1999; Bergström and Jansson 2000). It is not known if this stimulation is due to replacement of an aged AlloOC pool with fresh AlloOC or due to nutrient dynamics, quality differences between AlloOC exported during different flow conditions, or something else.

On the extreme end of the AlloOC bioavailability continuum, LMW organic substances used on very short timescales are found, such as carboxylic acids, simple carbohydrates and free amino acids. In forest ecosystems, the soil pool of LMW organic compounds has a turnover of several times per day and is responsible for a large part of the total carbon fluxes (Van Hees et al. 2005; Giesler et al. 2007). In aquatic ecosystems, much less is known about the importance of these compounds. There is, however, some indirect evidence for that LMW organic carbon of terrestrial origin can be a substantial subsidy to aquatic metabolism (Covert and Moran 2001; Jonsson et al. 2007; Ågren et al. 2008a; Roehm et al. 2009a). It remains a challenge to determine the relative importance of LMW AlloOC as substrate for freshwater bacteria and to find the specific organic LMW compounds that can be consumed rapidly and with a high BGE.

The objective of this thesis is to elucidate the roles of landscape, hydrology, aging processes and substrate composition for the bacterial use of allochthonous organic carbon for respiration and growth in boreal freshwater systems.

**Aims of the thesis**

This thesis addresses the following questions:

Are there differences between different boreal landscape types in their support of aquatic bacterial metabolism via export of allochthonous organic carbon (AlloOC)?

Does hydrology regulate the potential of exported AlloOC for supporting bacterial metabolism?

How does aging of organic carbon in natural aquatic systems affect the use of AlloOC as substrate for bacteria?

Which chemical fractions of AlloOC contribute the most to its use by bacteria?
Study area

The studies included in the thesis were conducted on streams and lakes in the boreal part of Sweden. AlloOC makes up more than 90% of the total organic carbon flux in lakes and rivers of this region (Algesten et al. 2004) and nearly 100% in many headwater streams (Schumacher et al. 2006). Because of this vast dominance of AlloOC, the area was suitable for studies of aquatic bacterial respiration and growth based on subsidies of terrestrial origin.

Papers I, II, and IV present studies from the Krycklan catchment at the Vindeln Experimental Forests (64˚14´N, 19˚46´E), where hydrological and biogeochemical studies have been performed for several decades (Köhler et al. 2008). A total of nine streams draining areas of different characters were selected. Paper III is based on a study in the Björntjärnarna catchment (64°07´N, 18°47´E), which is a sub-catchment of the well studied Lake Örträsket (Jansson et al. 1996). I studied two nested lakes, Upper and Lower Lake Björntjärnen, mainly receiving terrestrial drainage from a single headwater stream of three km in length. The lakes were relatively deep (8-10 m), in relation to their surface areas (0.03-0.05 km$^2$), and thermally stratified during summer. All study sites were dominated by AlloOC.

Forests, mires and surface waters collectively covered approximately 100% of the catchments. The forest component of the catchments was dominated by Norway Spruce (Picea abies). Mires were dominated by peat forming Sphagnum species and could be categorized as ombrotrophic or oligotrophic minerogenic. On average, the annual precipitation of the region is 600 mm, of which 35% falls as snow between November and April (Löfvenius et al. 2003). All the snow stored in winter melts during a two month period in spring, resulting in an annual flood that carries 50% or more of the total annual discharge and AlloOC transport (Laudon et al. 2004; Buffam et al. 2007).

Methods

Sampling of streams of different characters in the Krycklan catchment was carried out 2005-2007 on a total of 14 dates, at varying season and flow. The Björntjärnarna lakes were sampled during a seasonal cycle 2006-2007. Analyses of bacterial use of AlloOC were performed using a bioassay approach (I-IV). While in situ bacterial metabolism fluctuates in response to temperature (Apple et al. 2006), oxygen concentrations (Cole and Pace 1995), light climate (Lindell et al. 1995) and various other factors, the bioassays approach makes it possible to measure to potential of AlloOC for supporting bacterial metabolism under controlled laboratory conditions. Natural water samples were equilibrated with a standard air mixture and subsampled into multiple small (22 ml) gas tight glass bottles, leaving a headspace flushed with standard air. All bottles were incubated in the dark at 20°C during periods of up to 14 days. During the incubations, BP was analyzed repeatedly with the leucine incorporation method (Smith and Azam 1992; Karlsson et al. 2002) and BR as CO$_2$ production using gas chromatography.
Analyses of carbon, nitrogen and phosphorus fractions were performed using standardized methods. The organic carbon was further characterized by measuring its ultra-violet absorbance (I-IV), fluorescence (III) and contents of carboxylic acids, free amino acids and simple carbohydrates (IV).

The spatial (landscape) regulation of BR, BP and BGE was evaluated using partial least square (PLS) regression analysis with catchment characteristics and stream physicochemical properties as predictors (I). Hydrological control of bacterial metabolism in streams was assessed by a two-source linear mixing model describing how AlloOC source (miire or forest) is dependent on discharge (II). A model for average AlloOC age (time span from soil discharge to observation) was developed in order to analyze BR, BP and BGE in relation to aging of AlloOC during its residence time in lakes (III). Finally, bacterial metabolic processes were analyzed in relation to consumption of specific LMW organic compounds (IV).

**Landscape regulation of aquatic bacterial metabolism**

Drainage from different boreal landscape components showed clear differences in organic carbon concentration and character (I-II and IV). AlloOC concentrations were 7-47 mg C L⁻¹, with the lowest values in streams with forested catchments and the highest in streams with mire-dominated catchments. While AlloOC concentrations of mire and forest drainage converged to intermediate values at discharge peaks (II; see section ‘The role of hydrology…’), differences between the two sources in AlloOC bulk characters were similar for all hydrological conditions. The ratio between absorbance at 254 and 365 nm (Strome and Miller 1978; Dahlén et al. 1996), which can be used as a proxy for AlloOC contents of LMW compounds (IV), was significantly higher in forest (4.5-5.2) compared to mire (3.8-4.4) streams (I-II and IV). Organic material C/P and C/N ratios indicated that AlloOC from forests comprise chemical structures with higher contents of P and N, in comparison with AlloOC from mires (I).

Rates of bacterial respiration (BR) were 30-309 µg C L⁻¹ d⁻¹ (I-IV). The main predictor of BR was the concentration of AlloOC, which was positively correlated (R² = 0.52-0.78) in all data sets (shown in II-III). These relationships suggest that AlloOC support of aquatic BR is proportional to the export of organic carbon, which generally is the highest from landscapes with high wetland coverage (Schiff et al. 1998) or with highly branched stream networks (Ågren et al. 2007) which have large carbon-exporting riparian areas (Bishop et al. 2004). However, I found no consistent couplings between BR and AlloOC source/character, or between BR and nutrient concentrations (I-IV). Moreover, BR showed remarkably little variation expressed per unit of AlloOC (2-fold), compared to in absolute numbers (10-fold; II). The variation found in carbon specific BR, though relatively small, was explained by catchment size and pH (see PLS model in I). Possibly, a smaller share of the AlloOC could be used for BR because of low pH in the smaller study streams, e.g., causing enzyme denaturation or hydrolyzation of cell components (Atlas and Bartha 1997).
Both absolute and carbon specific bacterial product ion (BP) varied more than 20-fold with values of 4-94 µg C L$^{-1}$ d$^{-1}$ and 0.02-0.63% d$^{-1}$ (I-IV). Initial incubation values of absolute as well as carbon specific BP correlated positively ($R^2 = 0.51-0.58$) with the catchment forest coverage (Fig. 3 in I) and negatively with catchment mire coverage. Ultimately, this means that although mires may contribute with the major part of the total organic carbon export, forests can contribute with most of the carbon that is used for BP on a short-term scale (Ågren et al. 2008a). BP was also positively correlated with the 254/365 nm absorbance ratio ($R^2 = 0.39-0.50$), which suggests that BP was regulated by AlloOC quality properties mediated by different landscape components (II). Inorganic nutrient enrichment (N or N+P) stimulated BP in forest but not in mire drainage samples (I). However, there were no correlations between BP and natural variations in N or P fractions (I-III) signifying that the natural nutrient variations were too small to affect BP. Alternatively, N and P adsorption by AlloOC may have decoupled measured nutrient variables from actual nutrient bioavailability (Jones et al. 1993; Stepanauskas et al. 2000). The PLS regression suggested catchment forest coverage and pH as the two major (positive) regulators of BP (I).

The bacterial growth efficiency (BGE) was 0.06-0.51 (I-IV) and showed strong positive correlations to forest coverage ($R^2 = 0.61-0.78$); particularly when measured at the initial stage of the incubations (Fig. 3c in I). Of the different metabolic measures, BGE also showed the strongest dependence on AlloOC character. The PLS regression model explained 88% of the variability in BGE and most of the explained variation was due to positive relationships to the 254/365 nm absorbance ratio and to the forest coverage, and negative relationships to the AlloOC quality measures C/P and C/N (I). In paper II, the absorbance ratio alone explained 63% of the variation in BGE. Like BP, BGE in forest drainage was stimulated by nutrient enrichment (I), although BGE was not directly affected by natural variations in N or P concentrations (I-III).

**The role of hydrology for export of substrates for bacteria**

Combining all study streams, BR and BP showed weak but significant positive correlations with log specific discharge ($R^2 = 0.13$ and $0.21$, respectively; II). A partial correlation analysis showed that the correlation with BR, however, was attributable to changes in the AlloOC concentration only, and not to AlloOC character. Analyzing the different stream types one by one, a different pattern appeared. In streams with mixed catchments (forests and mires in typical proportions), measures of bacterial metabolism and AlloOC character showed values close to those of mire streams during low flow and close to those of forest streams during high flow (II). The values from forest and mire streams, on the other hand, were similar during all flow conditions. Thus, there were very strong correlations between log specific discharge and, e.g., BGE ($R^2 = 0.76$) and carbon specific BP ($R^2 = 0.85$), exclusively in the ‘mixed’ streams. These results suggest that hydrological control of bacterial metabolism is mainly mediated by shifts between the relative importance of mires and forests as organic carbon exporters.
During low specific discharge (1 L s\(^{-1}\) km\(^{-2}\)), there was a ratio between areal organic carbon export from mires and forests of ca 5, but with increasing discharge, this ratio approached 1 (II). The result agrees with previous studies from the region showing that high AlloOC concentrations in mire streams and low AlloOC concentrations in forest streams converge to similar values during discharge peaks (Laudon et al. 2004; Buffam et al. 2007). Mechanistically, the pattern can be explained by rising groundwater levels in forested areas which activate new soil organic carbon sources, thus increasing forest stream AlloOC concentrations (Bishop et al. 2004). In contrast, no new sources are activated in the mires, where instead increases in overland runoff may dilute stream AlloOC concentrations (Petrone et al. 2007). BGE in forest and mire drainage sampled from soil water showed stable values with means of 0.39 and 0.14, respectively. Corresponding values for carbon specific BP (% d\(^{-1}\)) were 0.30 and 0.07. Applying these values as forest and mire end members in a linear two source mixing model (Fig. 5 in II), stream values of BGE and carbon specific BP could be estimated based on the known mixing of AlloOC from forest and mire sources. This mixing model analysis explained >80% of the variation in both BGE and carbon specific BP.

In contrast to BGE and BP, BR was not affected by the differences in AlloOC character between forest and mire drainage (I-II) and could not be modeled based on hydrology-dependent mixing of AlloOC from the two sources (I). This result fits the general picture of BP being more variable and resource dependent than BR (Del Giorgio and Cole 1998; Lopez-Urrutia and Moran 2007). A wide range of natural compounds can be used for BR, but only substrates of high energy potential can support efficient bacterial growth, and only when essential inorganic nutrients are accessible (Russell and Cook 1995; Del Giorgio and Cole 1998). In addition, while the minimum BR of a bacterium must meet the energy requirements for cell maintenance, BP can proceed at highly variable rates depending on variations in the conditions controlling growth (Smith and Del Giorgio 2003; Lopez-Urrutia and Moran 2007).

**Bacterial use of aged allochthonous organic carbon**

The potential of AlloOC for supporting metabolism changed significantly during the incubations (I-IV). BP and BGE were highest at the initial stage of the incubation, and decreased by 60-70% in the next 7 days (I-III). BR decreased insignificantly (I-II) or by ca 20% (III) during the same period. Simultaneously, there was a drop in the 254/365 nm absorbance ratio (Fig. 5 in I; Table 1 in IV) indicating a change in the AlloOC character, and a possible consumption of LMW substrates supporting efficient bacterial growth (IV). I interpret these changes as the result of short-term aging of the AlloOC pool (I) and argue that similar changes follow the loading of fresh AlloOC into boreal lakes (III). The model for calculating AlloOC average age in lakes and streams of the Björntjärnarna catchment (equations 1-2 in III) generated values from fractions of 1 d to a maximum of 173 d. BGE and BP decreased significantly with increasing AlloOC age (R\(^2\) = 0.27 and 0.38), but the correlations were considerably stronger after a
temperature correction of the AlloOC age (Table 1 in III). The temperature correction was performed by assuming that AlloOC aging was 2.5 times faster for every 10°C of increase in water temperature \((Q_{10} = 2.5)\). Even stronger relationships were obtained by modeling BGE \((R^2 = 0.54)\) and BP \((R^2 = 0.70)\) as exponential functions of the corrected AlloOC age (Fig. 4 in III). After two months of in situ AlloOC aging in 20°C, BGE and BP had decreased, from their initial values, by more than 50% (Fig. 4 in III).

Decreases in bacterial metabolism with aging of AlloOC during laboratory or lake in situ conditions were not caused by decreased nutrients availability. Contrary, enrichment of inorganic N and P to constant levels of excess revealed even stronger patterns of decreases in BGE and BP with increasing AlloOC age (I and III). Instead, the changes in bacterial metabolism were clearly coupled to changes in the character of AlloOC. In the Björntjärnarna lakes, there was a shift in organic carbon quality to a more aromatic and recalcitrant AlloOC character, as indicated by a rise in specific UV absorbance (III). There was also a slight increase in the McKnight fluorescence index with increasing AlloOC age (Mcknight et al. 2001), indicating a parallel autochthonous carbon contribution in the lakes (III). However, the possible phytoplankton stimulation of BGE and BP (Del Giorgio and Cole 1998) was too small to balance the negative effects on BGE and BP caused by aging and processing of labile allochthonous substrates (III).

These results pinpoint the importance of hydrological temporal and spatial variation in combination with lake size (water renewal time) for replacing aged AlloOC pools in boreal freshwaters with young AlloOC pools that can support efficient bacterial growth (Wikner et al. 1999; Bergström and Jansson 2000). The role of BP for energy mobilization in unproductive lakes (Jansson et al. 2007) implies that conditions which determine aquatic AlloOC age can have considerable spin-off effects on the structure and function of pelagic food webs.

Fractions of AlloOC supporting efficient metabolism

The spectrophotometric properties of AlloOC (254/365 nm ratio) consistently indicated that higher BGE and BP in forest drainage were coupled to consumption of low molecular weight (LMW) compounds (I-II and IV). Further support for this indication was given by direct measurements of carboxylic acids, free amino acids and simple carbohydrates during bioassays of AlloOC from different sources (IV). Total concentrations of LMW AlloOC, defined as the sum of measured LMW fractions, were 0.56-1.01 mg C L\(^{-1}\) in the forest drainage and 0.39-0.43 mg C L\(^{-1}\) in mire drainage. Thus, despite higher total AlloOC export from mires, there were on average twice as high concentrations of LMW organic compounds in forest drainage, compared to in mire drainage.

A variety of carboxylic acids, amino acids and carbohydrates were significantly assimilated by bacteria, meeting 15-17% of the bacterial carbon demand for BR and BP in mire stream samples, and 50-100% of the carbon demand in forest stream samples. The LMW AlloOC concentration explained most of the observed variation in bacterial
growth efficiency ($R^2 = 0.66$; IV). Of the 29 chemical species that was detected, acetate was the most important, representing 45% of the total bacterial consumption of all LMW compounds. The unproportionally large effects of LMW compounds (high share of bacterial use of carbon despite the low share of total AlloOC) means that LMW AlloOC can be an important base for bacterial production in boreal streams and lakes, especially during and after high flow episodes when large amounts of organic carbon are exported from terrestrial systems (III-IV). I calculated that LMW organic compounds in boreal spring flood drainage could potentially support all in situ bacterial production in receiving lake waters during periods of weeks to months after the spring flood (IV).

**Concluding remarks**

Results presented in this thesis show that landscape, hydrology and organic carbon aging have large influence on the bacterial use of allochthonous organic carbon in boreal aquatic systems. The highest bacterial production and growth efficiencies were found in fresh samples of forest drainage and the lowest in mire drainage and aged samples (laboratory or *in situ* aging). High flow episodes increased the export of organic carbon from forests, in relation to the export from mires, stimulating the bacterial production and growth efficiency in streams with mixed (forest and mire) catchments. Much of these patterns can be explained by forest export of labile low molecular weight organic compounds, consumed rapidly and with high growth efficiency by aquatic bacteria. However, in contrast to bacterial production, the bacterial respiration was proportional to AlloOC concentrations and did not seem to be affected by the organic carbon composition. Considering the role of bacterial production as a base for heterotrophic food chains, bacterial metabolism based on allochthonous organic carbon can have considerable effects on the structure and function of boreal aquatic ecosystems.

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