Regulation of carbon dioxide emission from Swedish boreal lakes and the Gulf of Bothnia

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Abstract

The global carbon cycle is subject to intense research, where sources and sinks for greenhouse gases, carbon dioxide in particular, are estimated for various systems and biomes. Lakes have previously been neglected in carbon balance estimations, but have recently been recognized to be significant net sources of CO_2.

This thesis estimates emission of carbon dioxide (CO_2) from boreal lakes and factors regulating the CO_2 saturation from field measurements of CO_2 concentration along with a number of chemical, biological and physical parameters. Concentration of dissolved organic carbon (DOC) was found to be the most important factor for CO_2 saturation in lake water, whereas climatic parameters such as precipitation, temperature and global radiation were less influential. All lakes were supersaturated with and, thus, sources of CO_2. Sediment incubation experiments indicated that in-lake mineralization processes during summer stratification mainly occurred in the pelagial. Approximately 10% of the CO_2 emitted from the lake surface was produced in epilimnetic sediments.

The mineralization of DOC and emission of CO_2 from freshwaters was calculated on a catchment basis for almost 80,000 lakes and 21 major catchments in Sweden, together with rates of sedimentation in lakes and export of organic carbon to the sea. The total export of terrestrial organic carbon to freshwaters could thereby be estimated and consequently also the importance of lakes for the withdrawal of organic carbon export from terrestrial sources to the sea. Lakes removed 30-80% of imported terrestrial organic carbon, and mineralization and CO_2 emission were much more important than sedimentation of carbon. The carbon loss was closely related to water retention time, where catchments with short residence times (<1 year) had low carbon retentions, whereas in catchments with long residence times (>3 years) a majority of the imported TOC was removed in the lake systems.

The Gulf of Bothnia was also studied in this thesis and found to be a net heterotrophic system, emitting large amounts of CO_2 to the atmosphere on an annual basis. The rate of CO_2 emission was depending on the balance between primary production and bacterial respiration, and the system was oscillating between being a source and a sink of CO_2.

Key words: lakes, boreal, Gulf of Bothnia, CO_2, NEE, DOC, mineralization, sediment, catchment, net heterotrophy

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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:

I Sobek S, Algesten G, Bergström A-K, Jansson M, Tranvik, LJ (2003) The catchment and climate regulation of pCO_2 in boreal lakes. *Global Change Biology* 9: 630-641.

II Algesten G, Sobek S, Bergström A-K, Jonsson A, Tranvik LJ, Jansson M. Contribution of sediment respiration to summer CO_2 emission from boreal and subarctic lakes. *Submitted*.

III Algesten G, Sobek S, Bergström A-K, Ågren A, Tranvik LJ, Jansson, M (2004) Role of lakes for organic carbon cycling in the boreal zone. *Global Change Biology* 10:141-147.

IV Algesten G, Wikner J, Sobek S, Tranvik LJ, Jansson M (2004) Seasonal variation of CO_2 saturation in the Gulf of Bothnia: Indications of marine net heterotrophy. *Global Biogeochemical Cycles* 18, GB4022, doi: 10.1029/2004GB002230.

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INTRODUCTION

One of the major environmental issues of the century is the risk of an increased greenhouse effect leading to increasing global air temperatures, which in turn may promote other changes of the climate, such as changed precipitation patterns, redirection of ocean currents and meltdown of glaciers (Houghton 1997). Vast amounts of greenhouse gases (GHG) are produced in the world, both from natural and anthropogenic sources, and are released to the atmosphere increasing the retention of longwave radiation in the atmosphere (Bonan 2002). There are several GHG´s, such as water vapour, carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O). CO_2 is the most widely discussed greenhouse gas despite the fact that CH_4 and N_2O are more efficient in absorbing infrared light (21 and 206 times the greenhouse gas effect of CO_2) but these gases occur in much lower concentrations in the atmosphere (1.7 and 0.3 ppm respectively compared to 365 ppm for CO_2; Bonan 2002). CO_2 concentration, as well as the concentration of all GHG´s, has increased rapidly in the atmosphere (present CO_2 concentration is about 365 ppm compared to pre-industrial (year 1760) concentration of ca. 280 ppm; Bonan 2002). It is more and more accepted among researchers that this increase is affecting the climate. Efforts are made to construct climate models based on future emission scenarios of GHG´s to the atmosphere (e.g. Jones *et al*. 2004). It is, therefore, important that the fluxes of CO_2 from, and between, different pools on earth are well known, and that potential sources and sinks of CO_2 can be identified.

The boreal forest zone covers approximately 32 % of the Earth's forest areas (Burton *et al*. 2003), and aquatic systems and wetlands are important parts of the boreal biome (Bhatti *et al*. 2003). Lakes and peatlands cover about 20% of the boreal area, and rivers and ponds cover additionally 10% (Apps *et al*. 1993). The boreal forest biome is characterized by a short growing season, a low mean temperature and forests dominated by coniferous species (Burton *et al*. 2003). The boreal forests and peatlands are enormous stores for organic carbon (265 and 415 Pg C respectively; Apps *et al*. 1993), which make the carbon balance of these systems particularly interesting. The boreal forest biome has traditionally been considered to be a net sink of carbon dioxide. However, the role of peatlands in the carbon cycle is under debate (e.g. Klarqvist 2001) and aquatic systems have not been considered at all.

Aquatic systems are not isolated ecosystems, but rather integrated subsystems in the landscape (Kling *et al*. 2000, Likens 2004, Soranno *et al*. 1999). High production of organic carbon in the terrestrial systems and a relatively low soil activity results in high concentrations of less degraded DOC in the soil water (Thurman 1985). Depending on climate, hydrology, morphometry (Rasmussen *et al*. 1989), drainage ratio (catchment area:lake area ratio), wetland coverage (Hope *et al*. 1996) and other catchment characteristics, allochthonous dissolved organic carbon (DOC) is imported from the catchment into streams and lakes. Boreal lakes are generally unproductive due to low levels of bioavailable nutrients, thus keeping primary production low (Jones 1992). The flow of organic matter in boreal lakes is, therefore, dominated by allochthonous DOC. Much of the allochthonous organic matter in boreal systems is composed of coloured humic substances (HS). The effects of input of coloured organic carbon are complex and faceted (Bergström 2000). For the focus of this thesis the most important impacts of HS are 1) the changes in light attenuation and temperature in surface water which follows from the light absorbance of HS, and 2) the input of HS as an external carbon, energy and nutrient source for aquatic heterotrophic bacteria.

The fate of the allochthonous DOC in lakes and other aquatic systems is primarily bacterial degradation of DOC (Cornett & Rigler 1987, del Giorgio *et al*. 1997). Boreal lakes, as previously mentioned, have low levels of bioavailable nutrients but also often high loads of allochthonous DOC. These factors in combination repress primary production (PP) and enhance bacterial production, meaning that bacterial respiration and production of CO_2 also will be higher (Carpenter *et al*. 1998, Hanson *et al*. 2003, Jones 1992). Bacterial respiration is the most important contributor to total respiration in aquatic systems (del Giorgio & Cole 1998) wherefore it is important to estimate. Depending on the ratio between organic carbon and bioavailable nutrients, the bacterial growth efficiency (bacterial biomass production/gross production; BGE) will vary. del Giorgio & Cole (1998) reported that BGE in natural waters varies between 1 and 60%, with the lowest values in oligotrophic waters. Smith & Prairie (2004) found that in lakes with different DOC and total phosphorous (TP), the BGE varied greatly (6.7-51.6%) and the variation was related only to TP and not to DOC. This result means that BGE is low in boreal lakes where the nutrient availability is low despite the fact that DOC concentration is high. Hence, a high input of organic carbon as an external energy source is not sufficient for high net bacterial production. Consequently, most of the bacterial exploitation of allochthonous DOC has CO_2 as the end product. Jansson *et al*. (2000) showed that unproductive lakes become net heterotrophic at DOC concentrations as low as 4-5 mg L^{-1} when bacterial respiration exceeds primary production, indicating that an increase in primary productivity will increase the span of autotrophy of the system (Duarte & Agustí 1998).

Another important degradation pathway for DOC is the oxidation by sunlight (Granéli *et al*. 1996, Miller & Zepp 1995). Photodegradation has been proved to be different for different pools of DOC and autochthonous organic carbon is less degraded than allochthonous DOC (Obernosterer & Benner 2004, Tranvik & Bertilsson 2001). The photodegradation can result in a direct production of CO_2 (Granéli *et al*. 1996) but it also modifies DOC to forms, which can enhance or reduce bacterial degradation on photobleached material, depending on the source of the organic carbon (Moran *et al*. 2000, Tranvik & Bertilsson 2001). Lindell *et al*. (1995) showed that bacterial biomass increased by several hundred percent when grown on UV-irradiated humic water. UV exposure is primarily suggested to split large humic macromolecules into smaller, more bioavailable units. Since the organic matter in boreal lakes is dominated by allochthonous DOC, the impact of UV-light is considered to enhance bacterial degradation of DOC and increase the production of CO_2 both directly and indirectly.

Particulate matter in lake water may be lost to sediments where it may be exposed for further degradation (Sed R), or be permanently incorporated in the sediment (Sed C, Figure 1). Most of the imported organic matter from terrestrial origin is in dissolved forms (DOC) and only about 5-10% of total organic carbon in boreal lakes (TOC) is considered to be in particulate form (Wetzel 2001).

The cycling of organic carbon and CO_2 in freshwaters of a boreal catchment is presented in Figure 1.

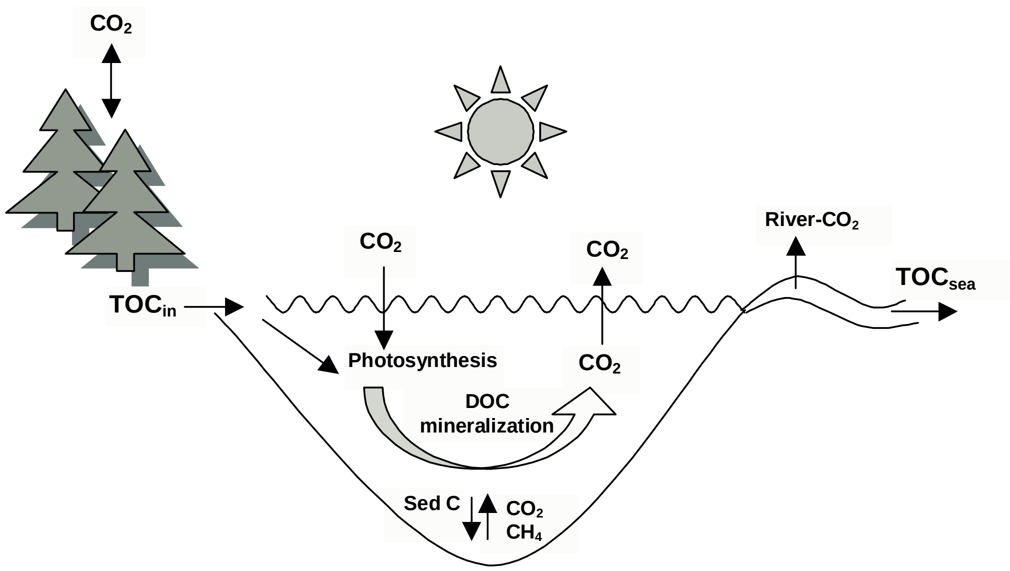

Figure 1. Cycling of organic carbon (total (TOC) and dissolved (DOC)) in freshwaters, from watershed input (TOC_{in}) to output to the sea (TOC_{sea}). Photosynthesis is input of organic material through primary production, and Sed C is loss of carbon (C) to permanent sediment incorporation. DOC mineralization incorporates both degradation by bacteria and light. River-CO_2 is mineralization and emission from running waters within the watershed.

During the last decade, several studies have reported carbon dioxide supersaturation in aquatic systems (Cole *et al*. 1994, Duarte *et al*. 2001, Kling *et al*. 1991). Cole *et al*. (1994) found that most lakes worldwide are supersaturated with CO_2, i.e. producing CO_2 which is subsequently released to the atmosphere. These lakes are considered to be net heterotrophic and sources of CO_2 since the mineralization and respiration processes exceed primary production (del Giorgio & Peters 1993, 1994).

Whether oceans are a sink or a source for CO_2 is widely debated (del Giorgio & Duarte 2002, Williams 1998) and a crucial matter for the carbon cycle since the oceans contain the largest pool of carbon on earth (ca. 38,000 Pg C; Post *et al*. 1990). The traditional view has been that oceans are autotrophic with P/R ratios >1 (del Giorgio & Duarte 2002) and the annual ocean carbon sink of anthropogenically released CO_2 to the atmosphere has been estimated to be 1.6-2.4 Pg C (Post *et al*. 1990, Siegenthaler & Sarmiento 1993). However, recent studies have shown that respiration in large parts of the oceans, especially in oligotrophic regions, exceeds production (Biddanda *et al*. 2001, del Giorgio *et al*. 1997, Duarte & Agustí 1998, Duarte *et al*. 2001). Organic carbon must, thus, be imported into oligotrophic waters to subsidise respiration. Possible inputs are from more productive marine systems and from terrestrial production via riverine input (Bauer & Druffel 1998, Meybeck 1982). Due to the wide gap of results from marine carbon balance studies, one problem to address in future research seems to be to resolve the balance between heterotrophic versus autotrophic marine systems.

It is possible to conclude that many aquatic systems represent net sources of CO_2 to the atmosphere. For boreal freshwater systems it is reasonable to regard all lakes and rivers as net heterotrophic. The reason of net heterotrophy is imported carbon. For freshwaters, the input consists of terrestrially derived organic carbon from the catchment and for marine systems the sources of excess carbon are contributions from productive nearby marine zones. However, there are several important aspects of aquatic system carbon fluxes that are unclear. For example, it is not clear which factors that regulate the lake mineralization of organic carbon and thus promote a CO_2 flux to the atmosphere. It is likewise not clear how different habitats in aquatic systems contribute to the overall production of CO_2 and to what extent the terrestrial carbon export is mineralised in lakes and marine systems.

The objective of this thesis is to elucidate several of these uncertainties concerning the role of aquatic ecosystems as net sources of CO_2 to the atmosphere.

AIMS OF THE THESIS

This thesis address the following questions:

- What factors are important for the carbon dioxide exchange between unproductive boreal lakes and the atmosphere?
- What is the role of sediments for the CO_2 emission and the carbon balance in boreal lakes?
- What is the retention of terrestrially exported organic carbon in boreal freshwater systems due to mineralization and sedimentation?
- Is the Gulf of Bothnia a net heterotrophic marine system?

STUDY AREA

The studies were conducted in lakes in boreal Sweden and the Gulf of Bothnia. This region covers climatic gradients in temperature (annual mean, –2 to 6 ºC), precipitation (500-800 mm) and length of the vegetation growth period (<100–200 days; National Atlas of Sweden) as well as lakes and a marine system with different DOC concentrations (2-30 mg L^{-1}). Catchments included are situated on precambrian bedrock with overlying till, and the area is dominated by coniferous forests, wetlands and lakes. Agricultural land is very rare and is often less than 1 % of the catchment area, and the majority of lakes are unproductive.

In **paper I**, 33 lakes in three regions situated along the climatic gradient in boreal Sweden were studied. The lakes were low-productive and varied substantially in size and humic content. For the study in **paper II**, 15 lakes in four regions including the subarctic, were selected. The study reported in **paper III** was based on the calculation for ca. 80,000 lakes in central and northern Sweden. The focus of **paper IV** was the Gulf of Bothnia which is the northern extension of the Baltic Sea (see Figure 2 for all study regions).

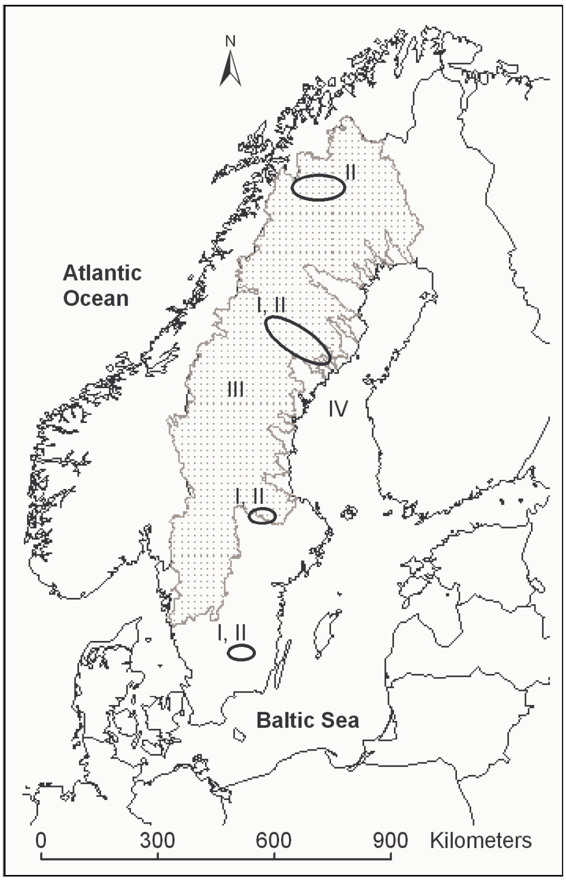

Figure 2. Research areas of the studies in this thesis. Roman numbers refer to the number of the papers in the thesis: I – three study regions, II – four study regions, III – ca. 80,000 lakes in the gray area in Sweden, IV – the Gulf of Bothnia.

METHODS

This work is based on measurements of CO_2 and other chemical and biological parameters in different aquatic systems. CO_2 concentration was measured with the headspace equilibrium technique (papers I, II and IV), and CO_2 emission was subsequently calculated by applying the equation for the gas exchange coefficient from Cole & Caraco (1998). CO_2 concentration in lake water was complemented with standard chemical and biological analyses, such as DOC, chl *a*, total nitrogen and phosphorus, absorbance (paper I) and primary and bacterial production (paper IV). Sediment net respiration was measured in one of the studies (paper II), where sediment cores were incubated *in situ* in transparent tubes. The concentration of dissolved inorganic carbon (DIC) and methane (CH_4) was analysed in the core water before and after incubation.

In paper III, carbon emission from lakes and rivers were calculated from data on total organic carbon (TOC) in roughly 2100 lakes and major rivers in boreal Sweden, after application of the regression between DOC and pCO_2 in boreal lakes (paper I). The loss rates were applied on ca. 80,000 lakes in Sweden. Permanent carbon loss to the sediments was calculated for the same lakes by the use of Finnish data on sedimentation rates in Finnish boreal lakes (Pajunen 2000). The transport of TOC to the sea was calculated from monthly mean data on TOC concentration and discharge from major river mouths. Terrestrial loss of TOC was assumed to be the sum of CO_2 emission from lakes and rivers, sedimentation of carbon and downstream transport of DOC to the sea (TOC_{in} = Lake-CO_2+River-CO_2+Sed C+TOC_{sea}; see Figure 1).

FACTORS REGULATING CO_2 EMISSION FROM LAKES AND THE GULF OF BOTHNIA

Due to the effects of allochthonous DOC in lake water it was expected that the CO_2 saturation in boreal lakes should be well correlated to DOC. There are studies which show a good correlation between CO_2 saturation and DOC in surface water of lakes (Hope *et al*. 1996, Riera *et al*. 1999), but no study has to our knowledge made a comprehensive analysis of the relative importance of additional factors for the CO_2 saturation in lakes. In **paper I** we assessed the role of numerous different factors for the partial pressure (pCO_2) and the saturation of CO_2 in boreal lakes. Thereby, we tested the possibility that climate factors like solar radiation, precipitation, temperature, latitude (Freeman *et al*. 2001, Hope *et al*. 1994, Schindler *et al*. 1997) and wind speed (Wanninkhof 1992), or other factors like lake and catchment morphometry (Rasmussen *et al*. 1989) and inorganic nutrient concentrations (del Giorgio & Peters 1994) could influence the DOC and its mineralization to CO_2 in lake surface water (Figure 3). Thirty three lakes in Sweden situated along a climatic N-S gradient were studied for this purpose. Water chemistry was sampled four times during the course of a year (summer stratification, autumn circulation, winter stratification and spring circulation) and weather data (wind speed, air temperature, global radiation, precipitation) were assembled from the Swedish Meteorological and

Hydrological Institute (SMHI). The data were analysed using multivariate statistics (partial least square analysis, PLS).

DOC was the most important variable determining pCO_2-variation in the boreal lakes. All lakes were supersaturated with CO_2 on all sampling occasions with only one exception. The DOC-concentration in the lakes ranged from 4 to 32 mg L^{-1}. The correlation between pCO_2 and DOC was similar for all regions during the whole open-water season. This was also evident in the PLS analysis where climatic parameters such as temperature, solar radiation, precipitation, wind speed and latitude had little influence on the concentration of CO_2 in surface waters. Only long-term precipitation had a moderate influence on the pCO_2. Catchment characteristics were more influential on pCO_2, e.g. drainage ratio, lake area and areal share of wetlands in the catchment, due to the influence of these characteristics on DOC concentration in freshwaters. A high drainage ratio (catchment area/lake area) implies a short residence time of the water and thus high concentrations of DOC (Kortelainen 1993, Rasmussen *et al.* 1989) and with increasing wetland area in the catchment the DOC load was even higher. The results suggested that the direct impact of air temperature differences on DOC mineralization and CO_2 emission was small. Temperature may have indirect effects by its importance on e.g. vegetation and thus the terrestrial export of DOC. However, such effects were evidently small within the temperature range represented in this study.

Allochthonous DOC is of importance also in marine systems (Bauer *et al*. 2002, Mackenzie *et al.* 1998). Low-productive marine systems have been found to be net sources of CO_2 to the atmosphere (Duarte & Agustí 1998, Duarte *et al*. 2001), indicating that organic carbon must be imported in order to produce a production:respiration ratio <1 (P:R ratio; Bauer & Druffel 1998, Gattuso *et al*. 1998). In **paper IV** it was shown that the Gulf of Bothnia was net heterotrophic on an annual basis, though no correlation between CO_2 saturation and concentration of DOC was found. The emission of CO_2 from the Gulf of Bothnia during the year was largely regulated by the balance between primary production and bacterial respiration in the mixed layer above the pycnocline. The surplus of organic carbon input needed to sustain the low P:R ratio and the supersaturation of CO_2 in the Gulf of Bothnia was not covered by riverine input of allochthonous DOC but other sources, e.g. input of DOC from the more productive Baltic Proper (Wulff & Stigebrandt 1989) was needed.

ROLE OF SEDIMENTS FOR THE CARBON BALANCE IN LAKES

Mineralization processes in lakes take place in the water column or in lake sediments. Many studies have been conducted in hypolimnion water and sediments to measure oxygen consumption and nutrient redistribution (Carignan & Lean 1991, Charlton 1980, Cornett & Rigler 1987, Jones & Simon 1980, Linsey & Lasenby 1985). Recently, studies have focused more on production of greenhouse gases in sediments (den Heyer & Kalff 1998, Liikanen *et al*. 2002, 2003), but there are few studies that have tried to relate sediment production of CO_2 to total CO_2 emission from lakes. Bacterial biomass and productivity are reported to be much higher in sediments than in water, and also nutrient and carbon concentrations are very high in the upper sediment (Sander & Kalff 1993). Therefore, it can be hypothesised that sediments can be important for the mineralization of organic carbon in lakes, and also for the emission of CO_2.

In **paper II** sediment net respiration (production of CO_2+CH_4 in sediment), as well as lake CO_2 emission and other chemical parameters in lake water and sediment, were measured during summer stratification in 15 boreal and subarctic lakes. The lakes had DOC concentrations between 2 and 25 mg C L^{-1}. All lakes but one was supersaturated with CO_2 in the surface water, and five lakes had negative net respiration rates (i.e. CO_2+CH_4 was consumed in the sediment). There was a good correlation between sediment respiration and DOC in the water, but no significant correlation to organic carbon content in the sediment surface (0-3 cm). There was, however, a weak positive correlation between sediment respiration and C:N ratio in the sediment ($r^2 = 0.35$, $p = 0.02$) where a low ratio indicates a high quality of the organic material. Allochthonous DOC dominates the flux of organic matter in these lakes and is characterized by a high C:N ratio. A stepwise multiple regression analysis showed that lake water DOC was the single most important parameter for the sediment net mineralization rate ($r^2 = 0.61$).

The mean ratio between sediment net respiration and total CO_2 emission for the study lakes was ca. 0.1, though the subarctic clearwater lakes stand out due to the very low DOC concentration (1.7-4 mg L^{-1}) promoting benthic primary production and net consumption of CO_2 in the sediments. However, the calculated pelagial respiration (total CO_2 emission minus sediment net respiration) was positive even in extremely clear lakes. This result is in agreement with results in Karlsson *et al*. (2002) where it was found that pelagic systems in clearwater lakes were dominated by bacterial energy mobilization from imported organic carbon, thus producing a net heterotrophic pelagic system.

AQUATIC C FLUXES IN RELATION TO TERRESTRIAL EXPORT OF ORGANIC C

Most boreal lakes are supersaturated with CO_2 and the degree of net heterotrophy is largely dependent on the concentration of DOC (paper I). To relate the magnitude of CO_2 emission from lakes to total transport of DOC in freshwaters, the total export of terrestrial organic carbon must be calculated. This allochthonous DOC is considered to be relatively refractory with low susceptibility to microorganisms. Short-term degradation experiments have shown that often less than 10% of the total organic carbon is degraded (e.g. Moran & Hodson 1990, Tranvik 1998). However, when measuring DOC mineralization during periods comparable to water retention times on catchment scales (years) the fraction of degradable DOC is much higher. Raymond & Bauer (2001) found that as much as 63% of riverine DOC was lost during a 1-year experiment. **Paper III** addressed the role of lakes for mineralization of allochthonous organic matter on a large scale (almost 80,000 lakes in central and northern Sweden). The emission from lakes was eight times the permanent sedimentation of carbon, and revealed that the most important loss factor of organic carbon was mineralization and subsequent emission. By comparing the flux of allochthonous DOC with primary production, the dominance of terrestrially produced organic matter in boreal freshwaters becomes clear. Calculated input of organic carbon by primary production was 80 times lower than total input of allochthonous TOC (Figure 3), emphasizing the dominance of external carbon in boreal lakes. The transport of TOC to the sea was about equal to the loss of organic carbon in freshwaters (emission of CO_2 from rivers and lakes and sedimentation) as a mean for all catchments (Figure 3). For individual catchments between 30 and 80% of the terrestrial losses of organic carbon were mineralised in freshwaters and emitted back to the atmosphere as CO_2 during the transport from terrestrial sources to the sea. The loss of TOC was strongly correlated to drainage ratio but above all to water residence time for the catchment. Low retention (<50%) was obtained in catchments where the water residence time was <2 year and high retention (>60%) in catchments with water residence time between 5 and 10 years. The result agrees well with Curtis (1998) who showed a similar relationship for individual lakes where the maximum DOC retention was close to 80%. Water residence time explained 81% of the variation for freshwater carbon retention in paper III, and the latitude (proxy for temperature) of the catchment only slightly increased the explanation of the retention (85%), implicating that hydrology is much more important than temperature for the degradation of DOC in boreal freshwaters.

As previously mentioned, the sediment net production of CO_2+CH_4 was a much smaller carbon flux than the flux of CO_2 to the atmosphere (mean loss rate 0.3 g C m^{-2} yr^{-1}, compared to 2.4; Figure 3) indicating that lake sediments are not as important for carbon sequestration as proposed (Dean & Gorham 1998). Also, Kortelainen *et al*. (2004) estimated the carbon pool in boreal lake sediments to be much smaller compared to previous estimates (19-27 Pg compared to 120 Pg estimated by Molot & Dillon (1996)).

COMPARISON OF AQUATIC AND TERRESTRIAL CO_2 FLUXES

Boreal lakes and the Gulf of Bothnia are, as shown in this thesis, net heterotrophic systems acting as sources of CO_2 on an annual time-scale. The net release of CO_2 in aquatic systems is due to mineralization of organic carbon imported from terrestrial systems. The net flux of CO_2 from lakes (related to catchment area; **paper III**) were in the range 0.6-5.0 g C m^{-2} yr^{-1} and total terrestrial export of TOC varied between 3.1 and 8.5 g C m^{-2} yr^{-1} (mean values 2.3 and 5.3 g C m^{-2} yr^{-1} respectively; Figure 3). These aquatic fluxes are small compared to those generally reported for forested terrestrial systems (e.g. Ciencala *et al*. 1998, Valentini *et al*. 2002, Figure 3). However, the net flux of CO_2 from boreal forests (net ecosystem exchange, NEE) is the result of a delicate balance between photosynthesis and respiration. Consequently, there can be great uncertainties in estimating NEE due to the vast amounts of CO_2 in the processes of uptake and release (Valentini *et al*. 2000). Forest NEE also exhibit great variation depending on e.g. climatic factors (radiation patterns, precipitation, length of growing season), standing age, management practices and forest type (Curtis *et al*. 2002, Valentini *et al*. 2000), and current estimates on NEE from boreal forests span from being carbon sinks to carbon sources (-600 to 90 g C m^{-2} yr^{-1}, Figure 3; Apps *et al*. 1993, Ciencala *et al*. 1998, Valentini *et al*. 2000). Valentini *et al*. (2000) showed that NEE increased significantly with increasing latitude reflecting the impact of climate and anthropogenic activity on forest productivity and NEE. A significant part of the boreal landscape consists of mires (10-20%) with a considerably lower net *exchange*? of CO_2 than forests (Klarqvist 2001).

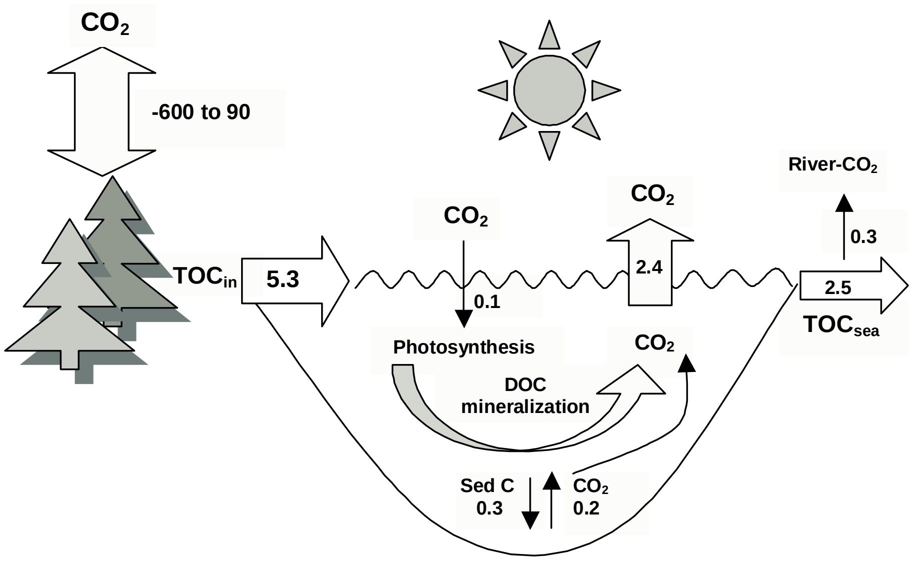

Figure 3. Mean fluxes of carbon in freshwater ecosystems estimated from ca. 80,000 lakes in 21 major catchments in northern Sweden (paper III), except for the sediment respiration which is estimated from 15 lakes in Sweden (paper II). Net ecosystem exchange of CO_2 (NEE) in boreal forests are estimates from several studies (g C m^{-2} yr^{-1}; forest estimates from Apps *et al*. (1993), Cienciala *et al*. (1998) and Valentini *et al*. (2000)). Forest flux ranges from being a sink (negative values) to a source (positive values). TOC_{in} = CO_2-emission (lake and river)+SedC+TOC_{sea}. All figures are related to the catchment area.

This thesis also demonstrates that approximately half of the terrestrial export of TOC to aquatic systems is returned to the atmosphere as CO_2. The other half was transported to the sea and the results from the Gulf of Bothnia (**paper IV**, Figure 4) showed that mineralization is likely to proceed in the marine environment.

It is therefore possible that high latitude lakes and coastal zones can be quantitatively important when considering the carbon balance of whole catchments, especially in areas with mature forests. It is recommended that the export of organic carbon from terrestrial to aquatic systems, and the subsequent fate of this carbon, is accounted for as a loss factor when estimating the NEE of the boreal zone.

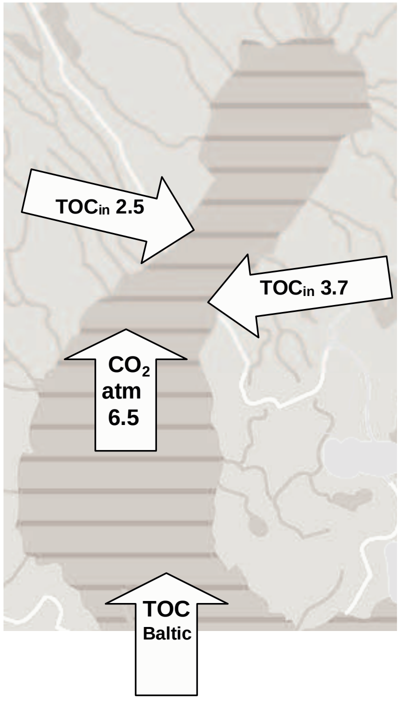

Figure 4. TOC input to the Gulf of Bothnia and CO_2 emission from the Gulf of Bothnia (Paper IV). TOC input from rivers (g C m^{-2} yr^{-1}) is related to catchment area of Swedish and Finnish rivers, respectively. CO_2 emission (g C m^{-2} yr^{-1}) is related to the entire catchment area. The size of the arrows are not according to scale, only indicating the relative size distribution. Data on input of TOC from Finnish rivers are from Pettersson *et al*. (1997).

SUMMARY

The resolution of the global carbon balance is one of the major issues of future climate research. In this thesis I have tried to reveal compartment carbon dioxide balances (lakes and Gulf of Bothnia) in order to complete the picture of the carbon balance in the boreal zone. Estimates are presented on CO_2 fluxes from boreal lakes and the Gulf of Bothnia and factors regulating the fluxes are discussed.

All sampled lakes, apart from a few exceptions, were supersaturated with CO_2, and DOC was the most important factor regulating the CO_2 concentration in lake water. Allochthonous DOC dominated the flow of organic carbon in the studied lakes. Even clearwater lakes (DOC<4 mg L^{-1}) were supersaturated, despite the low input of organic carbon and net autotrophic sediments, indicating that respiration rates of imported organic carbon in the pelagial were high enough to make most lakes net heterotrophic.

Calculations on loss of terrestrially produced organic carbon in boreal freshwaters revealed the importance of lakes for the removal of DOC through mineralization and emission of CO_2. Of the allochthonous TOC imported into lakes, 30–80% was withdrawn due to mineralization or sedimentation, and it was primarily water residence time within the catchments that controlled the retention of carbon.

The Gulf of Bothnia was found to oscillate between being a sink and being a source of CO_2 due to the variation in the balance between primary production and bacterial respiration (P/R ratio). Annually, the Gulf of Bothnia was an important source of CO_2 to the atmosphere compared to other areal fluxes in the boreal zone (Figure 4).

SAMMANFATTNING (Summary in Swedish)

En av de stora miljöfrågorna i vår tid är huruvida en ökad växthuseffekt, till följd av antropogena utsläpp av växthusgaser, påverkar vårt klimat i en takt snabbare än någonsin tidigare. Den mest diskuterade växthusgasen är koldioxid (CO_2) eftersom den finns i stora koncentrationer i atmosfären och har ökat dramatiskt under de seanste 150 åren. Mycket forskning pågår för att utröna eventuella källor och sänkor för CO_2 som finns på jorden, dvs vilka system som avger CO_2 till, respektive tar upp CO_2 från, atmosfären. Sjöar har tidigare inte varit inkluderade i kolbalansmodeller, men sedan det visat sig att sjöar är signifikanta nettokällor av koldioxid har sjöars roll lyfts fram i diskussionen. De marina systemens roll i den globala kolbalansen är under stor diskussion, och eftersom haven står för den största andelen av den globala kolreserven är det viktigt att etablera mer kunskap om kolbalansen i marina miljöer.

Denna avhandling presenterar resultat från studier av nettoutbytet av CO_2 från boreala sjöar. Majoriteten av boreala sjöar är nettokällor av CO_2 då de på årsbasis är övermättade med CO_2 i förhållande till atmosfärshalten (**Artikel I**). Det visade sig att koncentrationen av löst organiskt kol (DOC) i vattnet var den viktigaste faktorn att förklara variationen i CO_2-övermättnad. Varken koncentrationen av näringsämnen, fytoplanktonbiomassa, eller klimatiska faktorer hade någon större effekt på koncentrationen av CO_2 i sjöars ytvatten, och därmed emissionen av CO_2 till atmosfären. Då största andelen av DOC i boreala sjöar består av importerat terrestert producerat material är mineraliseringen i sjöar beroende på import av alloktont kol.

Med hjälp av sedimentinkuberinsförsök undersöktes sedimentens roll för produktionen av CO_2 i sjöar (**Artikel II**). Inkuberingarna utfördes under sommarstratifiering, och epilimnetiska sediment antogs bidra till koncentrationen av CO_2 i ytvattnet. Resultaten visar att produktionen av CO_2 och CH_4 i sedimenten var korrelerat med DOC-koncentrationen. Till skillnad från liknande studier fann vi inget samband med vattentemperatur eller näringshalter i sedimentet. Jämförelser med CO_2-emissionen från sjöytan visade att ca 10% av CO_2-produktionen ägde rum i sedimenten, medan den pelagiska mineraliseringen stod för den största delen.

För att utreda hur stor del av den terrestra exporten av organiskt material som mineraliseras och senare emitteras, eller som fastläggs permanent i sedimenten, utfördes beräkningar av CO_2-emission från sjöar och rinnande vatten, sedimentation i sjöar samt transport av totalt organiskt kol (TOC) till haven. Beräkningarna utfördes för nästan 80 000 sjöar i 21 huvudavrinnings-områden i Sverige (**Artikel III**). Av det terrestra organiska material som exporteras till ytvatten tar sjöarna bort i genomsnitt 50% (30-80%) under transport från källflöden till hav, och mineraliseringen av TOC var nästan 10 gånger större än sedimentationen. Retentionen av organiskt kol i ytvatten var starkt korrelerat till omsättningstiden av vattnet inom avrinnings-området, där en kort omsättningstid (<1 år) indikerade en låg retention (<30%), medan en längre retentionstid (>5 år) resulterade i en hög retention (>60-70%).

Säsongsvariationen av CO_2-emissionen från Bottniska viken undersöktes (**Artikel IV**) och resultaten visar att den är nettoheterotrof och källa för koldioxid på årsbasis, trots att ytvattnet under vissa delar av året är undermättat med CO_2. För att underhålla en högre respiration än fixering av CO_2 i vattenmassan, krävs en import av organiskt material från andra områden. I Figur 4 visas mängden importerat TOC från terrestert ursprung via svenska och finska älvar, samt införsel av marint producerat OC från det mer produktiva Egentliga Östersjön.

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