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Carbon Dioxide Supersaturation in Lakes – Causes, Consequences and Sensitivity to Climate Change

SEBASTIAN SOBEK

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Abstract
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The global carbon cycle is intimately linked with the earth's climate system. Knowledge about carbon cycling in the biosphere is therefore crucial for predictions of climate change. This thesis investigates the carbon dioxide balance of Swedish boreal lakes, its regulation, significance to the carbon budget of the boreal landscape, and sensitivity to climate change.

Swedish boreal lakes were almost exclusively supersaturated in CO_2 with respect to the atmosphere, resulting in an emission of CO_2 from lakes to the atmosphere. Lake pCO_2 was closely related to the concentration of terrigenous dissolved organic carbon (DOC), indicating that the utilization of terrigenous DOC by lake bacteria is a major source of CO_2. This conclusion is supported by independent field studies, showing that net plankton respiration accounts for most of the CO_2 emitted from Swedish boreal lakes, while photochemical mineralization and sediment respiration were less important.

Mineralization of terrigenous DOC and subsequent emission of CO_2 from lakes to the atmosphere was a major carbon loss factor in 21 major Swedish boreal catchments, removing 30-80% of the organic carbon exported from terrestrial soils to surface waters. Lake CO_2 emission is in the same order of magnitude as organic carbon accumulation in boreal forest soils, and should therefore be included in the carbon budget of the boreal landscape.

In a set of nearly 5000 global lakes, DOC concentration was a much more important regulator of lake pCO_2 than temperature. Climate change will therefore affect the carbon balance of lakes primarily via alterations in terrestrial DOC export, rather than via changes in temperature *per se*. Both current observations and models of future climate suggest an increasing export of terrigenous DOC from many Scandinavian catchments. Hence, there probably is a current trend towards higher CO_2 emission from Swedish boreal lakes, which is likely to continue in the future.

Keywords: carbon dioxide, boreal lakes, respiration, dissolved organic carbon, climate change

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Der Ball ist rund
Sepp Herberger

List of Papers

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

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

(V) Sobek, S., Tranvik, L.J. and Cole, J.J. 2005. Temperature independence of carbon dioxide supersaturation in global lakes. Global Biogeochemical Cycles 19: GB2003, doi:10.1029/2004GB002264.

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Contents

Abbreviations

CH_4	Methane
CO_2	Carbon dioxide
DIC	Dissolved inorganic carbon
DOC	Dissolved organic carbon
pCO_2	Partial pressure of carbon dioxide
Pg	Petagram, 10^{15} g
TOC	Total organic carbon
UV	Ultraviolet

Introduction

The global carbon cycle and climate change

Carbon is the major element of all life on earth. Photosynthetic organisms use light energy to convert carbon dioxide (CO_2) to organic carbon. Heterotrophic organisms derive energy from organic carbon and thereby oxidize it back to CO_2. Carbon is however not only part of biological transformations, but also involved in geological and chemical processes, such as weathering of carbonate rocks, CO_2 dissolving in sea water, and release of carbon gases by volcanic eruptions. Thus, carbon is exchanged between organisms, the sea, soils and the atmosphere, thereby linking the whole biogeosphere in the global carbon cycle.

The global carbon cycle is intimately linked to the earth's climate system, as both carbon dioxide and methane (CH_4) absorb infrared radiation, and thereby contribute to the greenhouse effect. Results from ice cores have revealed that atmospheric carbon dioxide was tightly coupled to mean global temperature during the last 740,000 years (EPICA community members 2004). Similarly, the transition from the extreme global warmth of the early Eocene climate 55 million years ago to the present glaciated state was closely coupled to the evolution of atmospheric CO_2 (Tripati et al. 2005). Hence, the current increase of atmospheric CO_2, which can be attributed to fossil fuel combustion and land use change, is likely to result in an increase in global mean temperature (IPCC 2001). There is a huge number of observations from different parts of the globe that confirm the current trend towards a warmer global climate. Accordingly, the Intergovernmental Panel on Climate Change (IPCC 2001) states that "the balance of evidence suggests a discernable human influence on global climate". This human influence mainly consists of alterations of the global carbon cycle, such as burning of fossil carbon and deforestation.

The role of freshwaters in the carbon cycle

A major obstacle in the assessment of the human influence on global climate is our limited knowledge of several aspects of the global carbon cycle, such

as the metabolic balance of the sea (Duarte and Agusti 1998; Williams 1998; del Giorgio and Duarte 2002; Karl et al. 2003), the extent of carbon fixation in Siberian forests (Schiermeier 2005), and the regulation of respiration in soils (Giardina and Ryan 2000; Knorr et al. 2005). The role of freshwaters in global carbon cycling is not only insufficiently understood, but above all totally neglected in global assessments. The latest report of the IPCC (2001) acknowledges the role of rivers as transport vehicles of carbon from land to the sea, but does not account for the often considerable transformation of carbon within freshwater systems.

Evidence accumulating during the last decade has led to an emerging picture of lakes as disproportionately important sites of carbon cycling. Lakes cover only around 0.5% of the earth's total area, but the sedimentation of organic carbon is almost half that of the oceans, which cover 71% of the earth's surface (Dean and Gorham 1998). At the same time, lakes emit CO_2 corresponding to 0.14 Pg C yr^{-1} to the atmosphere (Cole et al. 1994), which can be compared to the total terrestrial net sink of around 0.4 Pg C yr^{-1} (IPCC 2001). Furthermore, Bastviken et al. (2004) estimated that lakes emit more methane (CH_4) to the atmosphere than the ocean, corresponding to 6-16% of all natural CH_4 sources. In a regional study of the Amazon basin, emission of CO_2 from rivers and wetlands was an order of magnitude greater than riverine export of organic carbon to the sea (Richey et al. 2002). Considering the magnitude of these numbers, it is imperative to integrate freshwater systems into models of the global carbon cycle. There is however a lack of understanding of the mechanisms and regulations of carbon cycling in freshwater systems, preventing a more robust assessment of both the significance of freshwaters in the global carbon cycle, and the potential feedback of carbon cycling in freshwaters to climate change. The present thesis is a contribution towards a better understanding of the regulation, significance and sensitivity of CO_2 supersaturation in lakes.

Sources and sinks of CO_2 in lakes

The majority of the world's lakes are supersaturated in CO_2 with respect to the atmosphere, and consequently emit CO_2 to the atmosphere (Cole et al. 1994). The emission of excess CO_2 from lakes may be sustained by several processes, both biotic and abiotic (Figure 1).

CO_2 may be transported to lakes via surface water or groundwater flow, and subsequently emitted from the lake. Running waters, both streams (Hope et al. 2001) and rivers (Degens 1982; Cole and Caraco 2001), often display a high degree of supersaturation in CO_2, and may therefore be significant sources of CO_2 to lakes. Accordingly, Jones et al. (2001) reported that roughly 75% of the CO_2 emitted from Loch Ness in Scotland can be attributed to riverine inputs of CO_2 derived from soil respiration. On the other hand, Jonsson et al. (2001) found that import of CO_2 with surface water in-

flow was not a significant source of CO_2 in a large humic lake, in spite of the rapid renewal of the water in this lake by inflowing river water. Thus, although the input of CO_2 with inflowing surface water may be important in some lakes, CO_2 supersaturation can be maintained independently of inflow in other lakes.
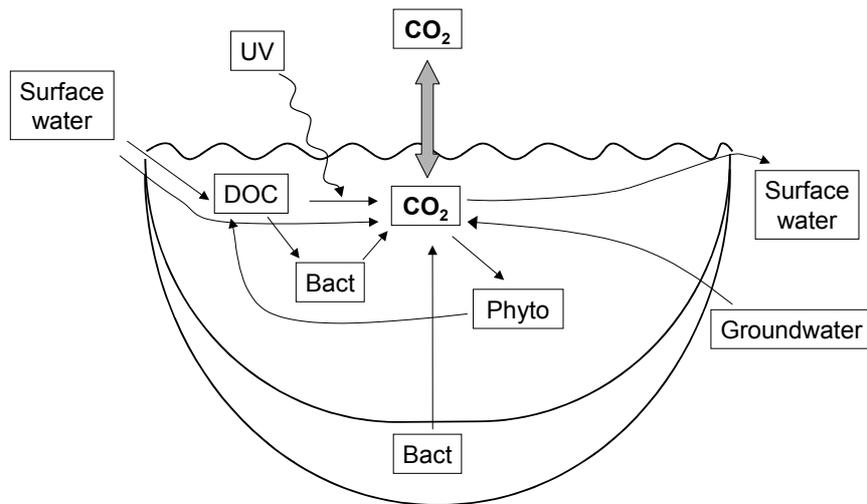
Figure 1. Simplified overview of CO_2 fluxes in lakes. DOC (dissolved organic carbon) is entering the lake from the catchment, and is released to the water by phytoplankton. DOC is mineralized to CO_2 by respiration of heterotrophic bacteria (Bact), or by photochemical reactions induced by UV radiation. Respiration of sediment bacteria releases CO_2 to the water. Inputs of CO_2 together with surface water and groundwater inflow contribute to lake CO_2. CO_2 is lost from the system via downstream transport or by uptake of phytoplankton (Phyto) during photosynthesis. The difference in CO_2 between the water and the air determines if CO_2 is leaving or entering the lake.

The import of CO_2 together with groundwater may also be a significant source of CO_2 in lakes (Striegl and Michmerhuizen 1998), as groundwater often is rich in CO_2 originating from both soil respiration and weathering of carbonate rocks. Lakes situated relatively low in the catchment generally receive higher groundwater input than headwater lakes (Cheng and Anderson 1994; Kratz et al. 1997b), and may therefore also receive high inputs of CO_2. The effect of groundwater-mediated inflow of CO_2 on the CO_2 of lakes is difficult to determine, since it is hard to quantify groundwater flows for a larger set of lakes, and groundwater inflow may be highly variable between

lakes, even if they are situated close to each other. Accordingly, Kratz et al. (1997a) failed to find a relationship between groundwater input and CO_2 concentration of six adjacent lakes in Wisconsin. Also, Wachniew and Rozanski (1997) reported that groundwater-mediated input of DIC was insufficient for maintaining the high DIC concentration in the water of a groundwater-fed lake. Groundwater-mediated inflow of CO_2 is therefore undoubtedly important in some cases, but it can probably not account for the consistently observed CO_2 supersaturation in lakes (Hanson et al. 2003).

Another abiotic source of CO_2 in lakes is photochemical mineralization of dissolved organic carbon (DOC). Photochemical reactions driven by solar UV radiation can remove DOC from the water column, either by direct photo-oxidation of DOC to CO_2 (Salonen and Vähätalo 1994; Granéli et al. 1996), or by cleavage of DOC molecules into low molecular weight compounds available for bacterial metabolism (Lindell et al. 1995; Wetzel et al. 1995; Bertilsson and Tranvik 1998). It has been shown that photochemical mineralization can account for a large proportion of the DOC loss from lake water (Dillon and Molot 1997; Vähätalo and Wetzel 2004), while other studies reported that photomineralization accounts for only about 10% of the total mineralization (Granéli et al. 1996; Jonsson et al. 2001). The significance of photomineralization depends on the source of the DOC, such that allochthonous DOC (i.e. DOC imported from the catchment) is preferentially photomineralized, while autochthonous DOC (i.e. DOC derived from lake biota) is preferentially mineralized by heterotrophic microbes (Obernosterer and Benner 2004). On the other hand, the irradiation of allochthonous DOC significantly stimulates bacterial growth, while irradiation of autochthonous DOC results in decreased availability to bacteria (Tranvik and Bertilsson 2001). Hence, photochemical reactions induce a complex array of effects in lakes, and even though photochemistry has been shown to be a major source of CO_2 in some lakes, its general importance for the overall mineralization of DOC in lakes is not well constrained.

Finally, CO_2 in lakes may also be the result of respiration by heterotrophic organisms. Bacteria are the most numerous group of heterotrophic organisms in lakes, and are therefore the most important contributors of biologically produced CO_2 (del Giorgio and Peters 1993; Jonsson et al. 2001). While some studies have suggested that primary production in lakes outweighs community respiration (Carignan 1998; Carignan et al. 2000), the balance of evidence suggests that community respiration is often higher than primary production, resulting in lakes being net heterotrophic ecosystems that consume organic carbon and produce CO_2 (Salonen et al. 1983; Tranvik 1989; del Giorgio and Peters 1994; del Giorgio et al. 1997; del Giorgio et al. 1999; Cole et al. 2000; Jansson et al. 2000; Jonsson et al. 2001; Cole et al. 2002; Karlsson et al. 2002; Prairie et al. 2002; Hanson et al. 2003; Jonsson et al. 2003; Hanson et al. 2004). The high extent of respiration in many lakes is fuelled by inputs of allochthonous DOC, a heterogeneous mixture of organic

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molecules exported from terrestrial soils and wetlands to lake waters. Generally, the DOC pool of lakes consists of a mixture of both autochthonous DOC (i.e. derived from lake biota) and allochthonous DOC (i.e. derived from land), but frequently a large proportion of the DOC is allochthonous. In boreal lakes in particular, allochthonous DOC consists to a large degree of highly stained humic matter, originating from the breakdown of coniferous and wetland vegetation (McKnight and Aiken 1998). Allochthonous DOC has been recognized as a major modifier of lake ecosystem structure and function, both serving as a substrate for bacterial growth (Tranvik 1988), and impeding photosynthesis due to its effective light absorption (Jones 1998). Accordingly, the pCO_2 of lake surface water has been shown to be correlated with the DOC concentration (Hope et al. 1996).

Hence, we can conclude that even though abiotic sources of CO_2 (input via ground- or surface water, photochemical mineralization) certainly can influence the pCO_2 of individual lakes, microbial respiration of allochthonous DOC is generally the main source of CO_2 in lakes. This implies that the frequent supersaturation of CO_2 in lakes (Cole et al. 1994) can largely be attributed to the net heterotrophic metabolism of lake ecosystems, and that the pCO_2 can be used as a proxy of lake net ecosystem metabolism.

Aims of this thesis

Research on carbon cycling in lakes has made remarkable progress during the past decade. When this work was planned in 1999, there was a still a lack of knowledge about the regulation and significance of CO_2 supersaturation in lakes. The aims of this thesis were therefore to

1. assess the CO_2 balance of wide set of Swedish boreal lakes and investigate its regulation,
2. estimate the contribution of plankton respiration, sediment respiration and photo-oxidation to CO_2 emission in these lakes,
3. assess the importance of lake CO_2 emission for the overall carbon balance of the Swedish boreal forest, and
4. make predictions of climate change effects on the CO_2 balance of lakes.

We chose to study boreal lakes because the boreal forest zone covers most of Sweden, 10% of the earth's land area, and is very rich in lakes. Thus, the results of our studies are not only relevant on a national level, but also to millions of lakes in Europe, Asia and North America.

Methods

Papers I-III are based on data acquired during field sampling and experiments, while Paper IV reports an extrapolation of our results and literature data to whole catchments. Paper V is based on data from the literature and from national lake inventories. In the following, I will describe the main methods for Papers I-III, while the methods used in Papers IV-V will briefly be mentioned in the Results and Discussion section.

Lake description

The lakes studied in this thesis are typical for boreal Sweden, and can thus be considered representative for a large population of lakes in Sweden. Most lakes are small to medium-sized, relatively shallow, and nutrient-poor (see Table 1 in Paper I). The catchments are dominated by precambrian bedrock overlain by till, and consist mainly of coniferous boreal forest, wetlands and lakes, while agricultural land is rare. Depending on the size of the catchment and the proportion of wetlands (Rasmussen et al. 1989; Kortelainen 1993), the studied lakes are subject to a variable degree of inputs of allochthonous organic matter. The differences in input and in-lake degradation of DOC among the lakes result in DOC concentrations ranging between 4 and 32 mg L^{-1}. For the sediment study (Paper III), we also included subarctic lakes, which is a common lake type in the northwest of Sweden. These lakes are situated in birch forest or above the tree line, and have on average clearer water and less DOC than the boreal lakes (see Table 1 in Paper III).

The partial pressure of carbon dioxide in surface water

The partial pressure of a gas dissolved in water denotes the escaping tendency of the gas. If the partial pressure of CO_2 (pCO_2) in water is greater than the pCO_2 in the air, this will induce a CO_2 flux from the water to the air. The flux rate is dependent on the gas exchange velocity k, which can be approximated from wind speed (Cole and Caraco 1998; Crusius and Wanninkhof 2003). As k is independent of wind at low wind speeds, which is a typical situation for the predominantly small boreal lakes, and pCO_2 of the air is

less variable than pCO_2 in the water, lake pCO_2 is the main driver of CO_2 flux between boreal lakes and the atmosphere.

For determination of the partial pressure of carbon dioxide (pCO_2) in surface water, we sampled the 0-0.5 m depth interval of the pelagic zone with a Ruttner sampler. Sample water was transferred to 1.2 L glass bottles, which were sealed with gas tight rubber septa. Two replicate bottles were taken at each sampling occasion. Bottles were stored in coolers in order to avoid light exposure and to minimize temperature changes. Measurements of pCO_2 were obtained by headspace equilibration (Hesslein et al. 1991) within 3 h after sampling. 50 mL of ambient air were added as a headspace gas to the 1.2 L bottles filled with lake water. The gas and water phases were equilibrated by shaking the bottles vigorously for 1 min, which was twice the time needed for thorough equilibration. The gas phase was extracted from the bottle with a plastic syringe and the partial pressure of CO_2 (pCO_2) was measured on a portable infrared gas analyzer (EGM-3, PP Systems). Two readings were taken from each bottle, thus we received two duplicated measurements of pCO_2 for each sampling occasion. The pCO_2 of ambient air, which was used for equilibration, was measured at each sampling occasion. From the sample measurements we calculated pCO_2 in the water via Henry's constant according to Weiss (1974) after corrections for atmospheric pressure and for the amount of CO_2 added to the bottles with headspace air.

Mineralization rates in water and sediments

This thesis presents mineralization rates by plankton respiration, photo-oxidation and sediment respiration, which are based on in-situ incubations of lake water and sediment. For an exhaustive description of the experimental set-up, please refer to Papers II and III. In order to measure mineralization rates, we used a gas chromatographic method that requires a much smaller volume of sample water compared to the measurement of pCO_2 in lake water by infrared gas analysis. As the CO_2 produced by mineralization readily reacts with water to form carbonic acid, we measured CO_2 as dissolved inorganic carbon (DIC), i.e. the sum of free CO_2, H_2CO_3, HCO_3^- and CO_3^{2-}. For the sediment study, we also measured methane (CH_4), which is the end product of mineralization under anoxic conditions. Sample water (20 mL) was extracted from the incubation container using a plastic syringe equipped with a gas-tight valve. Then, 10 mL headspace (ambient air) was introduced into the syringe, and the water was acidified (400 µl 2M HCl) in order to transfer all inorganic carbon species to CO_2. Water and air phases were equilibrated in the closed syringe by vigorous shaking for 1 min, the gas phase was extracted, and stored in evacuated vials. Measurements were made on a Shimadzu GC-14A gas chromatograph, equipped with a thermal conductivity detector (for CO_2) and a flame ionisation detector (for CH_4). The pCO_2 and pCH_4 of ambient air, which was used for equilibration, was

measured and corrected for. Mineralization rates in water were calculated by subtracting the mean DIC concentration prior to incubation from the mean DIC concentration after the incubation. Mineralization rates in sediments are based on changes of the sum of DIC and CH_4 during incubation.

Results and Discussion

The regulation of pCO$_2$ in boreal lakes
Paper I

We found that Swedish boreal lakes are generally supersaturated with CO$_2$ on a yearly basis, and that the pCO$_2$ is mainly a function of humic content, expressed as the DOC concentration (Figure 2). These results are based on a study of 33 representative Swedish boreal lakes of different humic content, covering one whole year. Lake pCO$_2$ was below atmospheric equilibrium at only 1 of 116 sampling occasions. The lakes were distributed in three different areas of boreal Sweden, covering a latitudinal gradient from 57° to 64°N, corresponding to 5°C difference in annual mean temperature. Contrarily to our expectations, we could not observe a difference in lake pCO$_2$ along this gradient. The relationship between DOC and pCO$_2$ was similar in all three sampling areas (Figure 2).

Along with the pCO$_2$ of surface water, we also recorded several water chemical parameters, catchment and lake characteristics, and meteorological parameters, and used them in a PLS regression analysis. The results from this analysis (see Figures 2 and 3 in Paper I) demonstrate that the properties of the catchment and the lake (% wetlands in the catchment, lake area, water turnover time, drainage ratio) were important predictors of the humic content of a lake, which in turn was the most important predictor of pCO$_2$ (Figure 2). Climatic factors (temperature, precipitation, season, UV radiation) were of very limited importance as predictors of pCO$_2$.

These results have several important implications. The tight correlation between allochthonous DOC and pCO$_2$ is an indicator of higher mineralization in lakes with high DOC concentration. It is unlikely that the relationship between DOC and pCO$_2$ is due to the import of CO$_2$ together with the allochthonous DOC, as pCO$_2$ is rapidly outgassed in streams (Dawson et al. 1995), while DOC is comparably well conserved during downstream transport. Also the import of CO$_2$ to the lake together with groundwater flow is unlikely to explain the correlation between DOC and pCO$_2$, because groundwater is often high in CO$_2$, but low in DOC (Curtis 1998). Thus, in-lake mineralization appears to be the most likely link between DOC and pCO$_2$. As we could not find a correlation between solar radiation and lake

pCO_2, we conclude that bacterial utilization of DOC as a substrate (Tranvik 1988) is the major process behind the correlation between DOC and pCO_2. Thus, the consistent supersaturation of CO_2 in Swedish boreal lakes is mainly a result of these lakes being net heterotrophic ecosystems. Furthermore, the dependence of lake DOC primarily on catchment characteristics, rather than on climatic properties, implies that the effects of climate change on the CO_2 balance of boreal lakes will be indirect, i.e. via changes in vegetation and hydrology, rather than direct, i.e. higher temperatures.
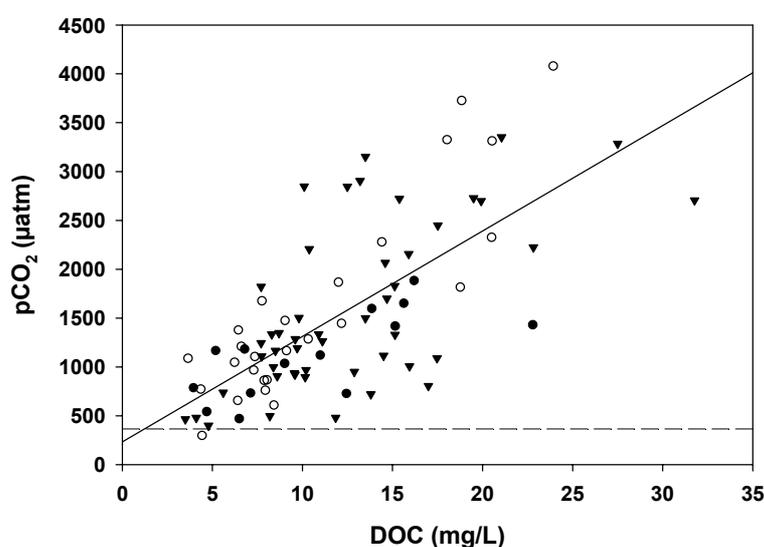

Figure 2. The relationship between DOC concentration and pCO_2 in the surface water of 33 boreal lakes during open-water conditions (spring, summer, autumn). Filled circles: Småland (southern Sweden); open circles: Bergslagen (middle Sweden); triangles: Västerbotten (northern Sweden). Solid line: linear regression, y=233.2+107.9*x; R^2=0.51. The dashed line depicts atmospheric equilibrium.

Sources of CO_2 in boreal lakes
Papers II and III

Results from Papers II and III indicate that plankton respiration is the most important source of CO_2 in lakes, while photo-oxidation and sediment respiration are of limited importance. Paper II compares plankton community respiration and photo-oxidation in two lakes, one clear-water and one humic, during midsummer conditions. We incubated sterile-filtered and 200 μm-filtered lake water in-situ in UV-transparent mesocosms, and measured the DIC production rates. In the clear-water lake, photo-oxidation contributed more to total mineralization in the water-column (41%) than in the humic

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lake (14%). Thus, net plankton respiration was a more important contributor to lake CO_2 production in the humic lake. In spite of these differences, total net mineralization in the water-column of the two lakes was similar. Solar irradiation was very high during the experiment, and therefore it can be expected that photo-oxidation will contribute less to whole-lake mineralization on a yearly basis. Thus, even if photo-oxidation at times can be significant, particularly in clear-water lakes (cf. Molot and Dillon 1997), its overall importance to mineralization of DOC in boreal lakes is probably limited, while plankton respiration appears to be the major source of CO_2 in the water-column (del Giorgio et al. 1999). This conclusion is further supported by other studies in boreal lakes. Jonsson et al. (2001) estimated that photomineralization accounts for around 10% of the whole-lake mineralization in a humic lake, and Granéli et al. (1996) reported that photo-oxidation is roughly 10% of plankton respiration.

In Paper III we assess the importance of sediment respiration to total mineralization and CO_2 emission from a series of 15 boreal and subarctic lakes of different humic content. Sediment cores were incubated in-situ at ambient light conditions, and mineralization was measured as the production of CO_2 and CH_4. Mean sediment respiration was calculated for the sediments that are in contact with the upper mixed layer. Both mean sediment respiration rate and CO_2 emission to the atmosphere were positively correlated to the dissolved organic carbon (DOC) concentration in the water (Figure 3), demonstrating that both whole-lake mineralization (cf. Figure 2 and Paper I) as well as sediment respiration are stimulated by inputs of allochthonous DOC. The linear regression lines in Figure 3 indicate that the contribution of sediment respiration to CO_2 emission from these 15 lakes is about 10%, even though this proportion is quite variable for individual lakes. Similar percentages were reported for the contribution of epilimnetic sediment respiration to total epilimnetic respiration (2-18%, den Heyer and Kalff 1998) and to total epilimnetic DOC mineralization (20%, Jonsson et al. 2001). Clear-water lakes (DOC < 5 mg L^{-1}) frequently exhibited negative sediment respiration rates, i.e. CO_2 consumption, which we ascribe to benthic primary production on the illuminated lake bottoms. Still, all clear-water lakes apart from one emitted CO_2 to the atmosphere. Hence, we can conclude that processes in the water-column contribute more to the exchange of CO_2 between boreal lakes and the atmosphere. Combined with the findings of Paper II, it becomes clear that respiration of the plankton community accounts for most of the CO_2 produced in boreal lakes. This conclusion is well supported by several other studies (del Giorgio and Peters 1994; del Giorgio et al. 1999; Jonsson et al. 2001; Prairie et al. 2002; Hanson et al. 2003), and adds further evidence that boreal lakes predominantly are net heterotrophic ecosystems.
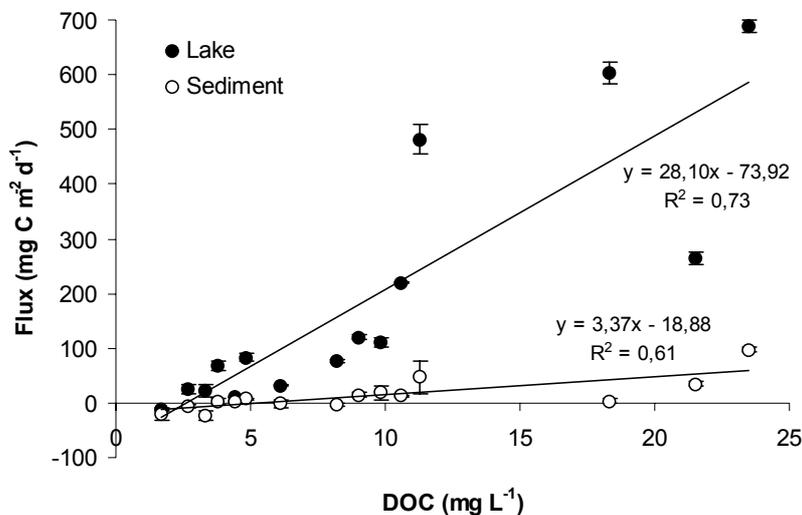
Figure 3. Fluxes of CO_2+CH_4 across the sediment (○) and the lake surface (●) for 15 boreal and subarctic lakes in relation to the DOC concentration in the lake water. The sediment flux is the mean respiration rate for sediments in contact with the mixed upper layer related to lake area. Error bars are SD.

CO_2 emission from lakes – does it matter?
Paper IV

We found that CO_2 emission from boreal lakes is a major loss factor in the organic carbon budget of the lakes themselves, in the export of terrestrial organic carbon by rivers to the sea, and probably also in the overall carbon balance of the boreal landscape. We arrived at these conclusions by using the relationship between pCO_2 and DOC (Figure 2) in order to predict CO_2 emission for all lakes in 21 major catchments in boreal Sweden. Lake CO_2 emission was then compared to other carbon fluxes by applying the following mass balance equation to each of the 21 catchments, which cover in total 316 100 km^2 and contain 79 536 lakes:

$$TOC_{export} = TOC_{sea} + S + E_L + E_R \qquad (1).$$

TOC_{export} is the export of total organic carbon (TOC, which consists to over 90% of DOC) from terrestrial soils to freshwaters, TOC_{sea} is the riverine export of TOC to the sea, S is permanent sedimentation of organic carbon, E_L is the CO_2 emission from lakes, and E_R is the CO_2 emission from rivers.

First, we expanded the dataset of Paper I with data collected by Jonsson et al. (2003) in lakes in northern Sweden. In the resulting dataset (n=136), TOC concentration explained 72% of the variability in pCO_2. Then, we used data

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from the Swedish lake register (www.smhi.se) and from the Swedish national lake inventory (www.ma.slu.se) in order to estimate CO_2 emission from all 79 536 lakes. 2120 lakes within the catchments are part of the national lake inventory, and for these lakes we could estimate pCO_2 from the TOC concentration. From pCO_2, we calculated the CO_2 emission from the 2120 inventory lakes according to Cole and Caraco (1998). Then, we used the national lake register, which lists and separates all lakes according to their surface area in five size classes. Combining the CO_2 emission and surface area of the 2120 inventory lakes with the lake register, we could calculate the average CO_2 emission for each size class. Multiplication with the total lake surface area covered by each size class in each catchment finally returned the total CO_2 emission of lakes in each catchment (E_L). In order to calculate the annual emission of CO_2, we accounted for the accumulation of CO_2 during ice cover, and the subsequent emission of CO_2 during ice melt.

The emission of CO_2 from rivers (E_R) was estimated from the area-weighted mean CO_2 emission from all lakes in the catchment, times the area covered by running water in each catchment. As rivers frequently have higher pCO_2 than lakes (Cole and Caraco 2001), our estimate of E_R is conservative. The incorporation of organic carbon in lake sediments (S) was calculated by applying net sedimentation rates of Finnish boreal lakes (Pajunen 2000). Riverine export of TOC to the sea (TOC_{sea}) was calculated from surveyed TOC concentration at the river mouths (www.ma.slu.se) and discharge (www.smhi.se).

We found that lake CO_2 emission was a major organic carbon loss factor in the 21 boreal catchments. Averaged for all catchments, lake CO_2 emission was about eight times higher than both organic carbon burial in sediments and CO_2 emission from rivers, and was roughly equal to riverine organic carbon export to the sea. Total loss of TOC in lakes (CO_2 emission + sedimentation) was roughly 30 times higher than the in-lake fixation of organic carbon by phytoplankton primary production, as estimated from published values of Swedish boreal lakes (see Paper IV). As lake CO_2 emission can largely be attributed to in-lake mineralization, this illustrates the high degree of net heterotrophy of Swedish boreal lakes. Depending on the water residence time of the catchment, between 30 and 80% (average 50%) of the TOC that is exported from terrestrial soils to freshwaters is mineralized in lakes and emitted to the atmosphere (Figure 4). The longer the water resides in the freshwater environment, the more DOC is removed by mineralization and sedimentation.
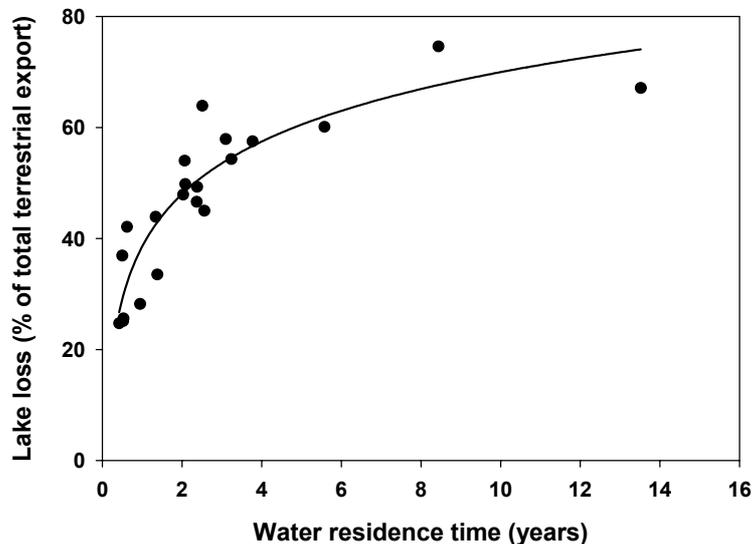
Figure 4. The loss of organic carbon in lakes (CO_2 emission + sedimentation), expressed as the percentage of total terrestrial export of organic carbon to freshwaters ($y=38.03+13.16*\ln(x)$; $p<0.001$; $R^2=0.81$). Each point in the plot represents one catchment.

The relative importance of lake CO_2 emission for the carbon balance of the boreal landscape depends primarily on the CO_2 balance of the forest. Net CO_2 uptake by boreal forests is typically two orders of magnitude higher than CO_2 emission by lakes (Cienciala et al. 1998; Gower et al. 2001; Markkanen et al. 2001). However, at a longer timescale (>100 years) most of the CO_2 fixed by trees will return to the atmosphere, as the harvested wood to a large extent will be burned or degraded. The crucial factor is therefore the proportion of the fixed CO_2 that is accumulated in forest soils. Typical carbon accumulation rates in boreal forest soils are in the same order of magnitude as lake CO_2 emission (Peltoniemi et al. 2004). If the export of TOC from forest soils to freshwater equals or exceeds the accumulation of carbon in terrestrial soils, as has been shown for the temperate Hubbard Brook catchment (Cole and Caraco 2001), CO_2 emission from lakes significantly affects the carbon balance of the boreal landscape. Furthermore, Valentini et al. (2000) showed that the net CO_2 uptake of forests decreases with increasing latitude, and may even be turned into a net CO_2 release in the northernmost forests. Hence, Paper IV demonstrates the necessity of integrating both aquatic and terrestrial carbon fluxes in order to correctly assess the exchange of CO_2 between the boreal landscape and the atmosphere.

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How will climate change affect the CO_2 emission from lakes?
Paper V

In order to assess the possible feedback of lake CO_2 emission to climate change, we analyzed pCO_2 in a large set of globally distributed lakes. From the results of this study, we predict that the CO_2 emission from lakes will depend much more strongly on changes in lake DOC concentrations, which are indirectly induced by climate change, while effects due to changes in water temperature *per se* will be less pronounced.

Climate change scenarios predict an increase in annual mean temperature of $2.5 - 4.5$ °C for Sweden during the next 100 years (www.smhi.se). This has implications for the biosphere, as temperature is a key controller of the physiology of organisms. In particular, respiration is more dependent on temperature than photosynthesis, which is likely to affect carbon fluxes in ecosystems (Allen et al. 2005). We therefore expected to find a gradient in pCO_2 in lakes along the 5°C gradient in annual mean temperature in Paper I. As evident from Figure 2, we could not find any consistent difference in pCO_2 of lakes from three climatically different regions in Sweden, indicating a lacking temperature effect. However, we could not exclude that the gradient in temperature might have been too short in order to detect any effect of temperature on lake pCO_2.

In order to base our predictions of climate change effects on a stronger and more representative dataset, we decided to expand the gradient in annual mean temperature. Using literature searches, national survey data and personal communication, we collected data on pCO_2 from 4902 global lakes, which is the so far largest collection of pCO_2 in lakes. Even though the data originate mainly from the temperate and boreal zones, the dataset stretches from high-arctic to tropical lakes, and therefore allows the analysis of large-scale climatic gradients on lake pCO_2. The spatial gradient may then be used to predict effects of temporal climate change. We fitted the lake data to global-scale databases on mean annual temperature and precipitation (New et al. 2000), runoff (Fekete et al. 2000), as well as soil carbon density (Global Soil Data Task Group 2000). The vast majority of lakes (93%) was supersaturated in CO_2 with respect to the atmosphere, which corroborates an earlier study by Cole et al. (1994).

We found that the concentration of DOC is a much better predictor of pCO_2 in lakes than is temperature. Both annual mean air temperature and in-situ water temperature explained very little of the variation in pCO_2 (6% and 0.3%, respectively), while DOC explained 26% (Figure 5). A multivariate analysis (partial least squares regression, PLS; total model $R^2=0.26$) confirmed that DOC is the single most important explanatory variable for pCO_2 in global lakes (Figure 6 in Paper V). Other potentially important variables

such as temperature, latitude, runoff, precipitation, soil carbon density and season did not add any significant explanatory power to the multivariate model. We attribute the fact that we do not reach a higher degree of explanation than 26% to short-term temporal variability of pCO_2 in lakes (Carignan 1998; Kelly et al. 2001), and the great diversity of lake ecosystems in terms of geographical, geological and hydrological setting, as well as basin shape, chemical composition of the water and biological communities. In spite of this great variability inherent in the world's lakes, DOC as a single factor explained 26% of the variation in pCO_2. As the DOC pool in lakes frequently contains a large proportion of allochthonous DOC, this provides evidence that DOC imported from the catchment is a globally important modifier of lake ecosystem metabolism. The lack of large-scale temperature control of lake pCO_2 may be explained by the concept of substrate and temperature as interacting regulators (Pomeroy and Wiebe 2001), meaning that the interplay between substrate supply and temperature ultimately regulates the net ecosystem metabolism of lakes. Thus, even if substrate supply to heterotrophic microbes (i.e. DOC) appears to be the dominating regulator of lake pCO_2 at a global scale, studies in specific individual lakes may show that temperature has a significant influence at the local scale.

In summary, we can predict that climate change will affect the pCO_2 of lakes not primarily by increased temperatures, but rather by changes in the landscape water balance, which will alter the export of DOC from terrestrial soils to lakes, the water retention time of lakes, and the formation of organic matter in soils. As lake pCO_2 is the main driver of the CO_2 flux between lakes and the atmosphere, this is even true for the emission of CO_2 from lakes. The key for understanding the feedback of lake CO_2 emission to climate change lies therefore in the terrestrial surroundings of the lakes. Climate models predict higher runoff in the northwest of Sweden (covering the largest part of the country), while runoff will decline in the southeast (Bergström et al. 2001), and changes in runoff will most likely be accompanied by corresponding changes in DOC export (Clair et al. 1999). In fact, there is evidence that the export of terrestrial organic carbon to freshwaters has increased in many parts of Scandinavia during the last decades, and that this increase is closely related to increases in precipitation or runoff (Forsberg and Petersen 1990; Forsberg 1992; Tranvik and Jansson 2002; Hongve et al. 2004). Thus, there probably is a current trend towards higher CO_2 emission from most Swedish boreal lakes, which is likely to continue in the future.
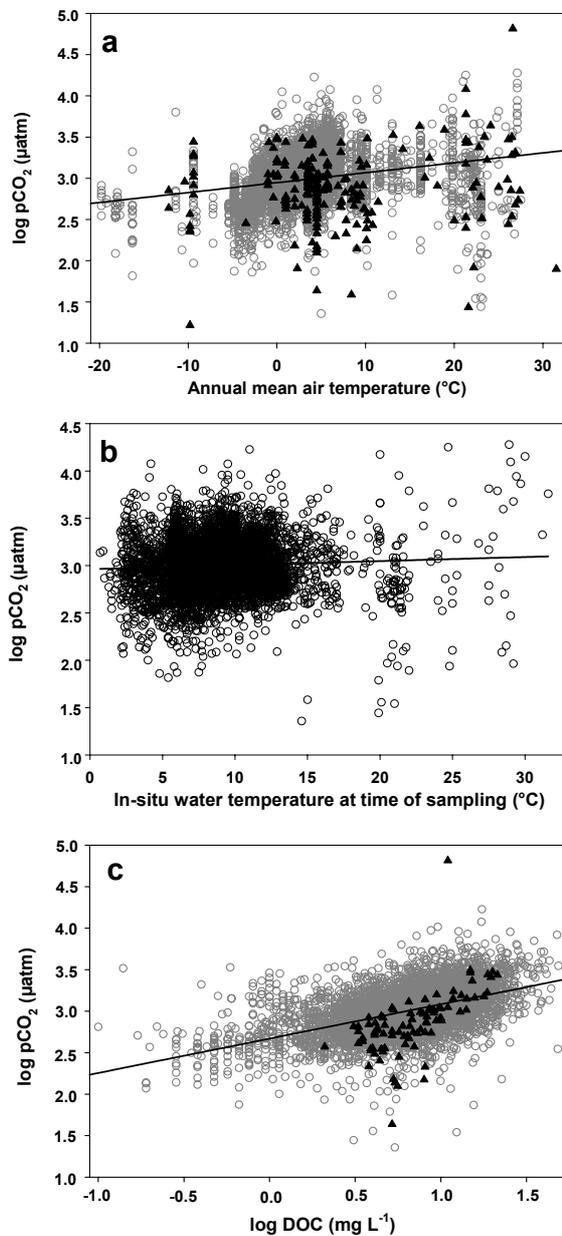
Figure 5. Linear regressions of log pCO_2 against a) mean annual air temperature ($y=2.95+0.012*x$, $p<0.0001$, $R^2=0.06$) b) in-situ water temperature at the time of sampling ($y=2.96+0.004*x$, $p<0.001$, $R^2=0.003$), and c) DOC concentration ($y=2.67+0.414*x$, $p<0.0001$, $R^2=0.26$). Each point in the plot represents one lake. Circles: lakes with one single measurement. Triangles: mean values for lakes with multiple measurements.
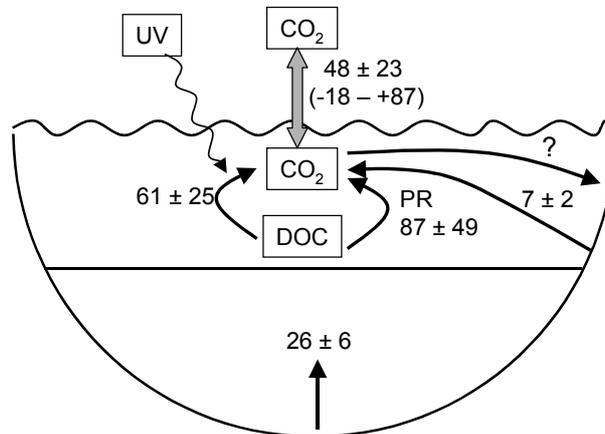
Klintsjön and Skärshultsjön – An example

The following chapter presents an example of in-lake CO_2 fluxes in two lakes, clear-water lake Klintsjön and humic lake Skärshultsjön, during summer stratification (Figure 6). These two lakes were studied in both Paper II and Paper III, and they are typical Swedish boreal lakes. The general patterns of carbon processing described below are therefore probably applicable to many other Swedish boreal lakes.

The clear-water lake Klintsjön (Figure 6a) is shifting between being a sink or a source of CO_2 to the atmosphere. Based on one measurement each summer from 2000 to 2003, the atmospheric flux of CO_2 ranged between -18 (uptake) and +83 (emission) mg C m^{-2} d^{-1}. On average however, Klintsjön emitted CO_2 to the atmosphere (48 ± 23 mg C m^{-2} d^{-1}; mean ± standard error). In the epilimnetic water-column, 61 ± 25 mg C m^{-2} d^{-1} were produced by photo-oxidation, and 87 ± 49 mg C m^{-2} d^{-1} by net plankton respiration. The considerable variation in plankton respiration is caused by subtraction and addition of other measured values, resulting in a growing error as the number of calculation steps grows. Epilimnetic sediments contributed with 7 ± 2 mg C m^{-2} d^{-1}, and hypolimnetic sediments released 26 ± 6 mg C m^{-2} d^{-1} to the bottom water. The epilimnetic sediment respiration rate is biased, because it is based on incubation of soft-bottom experiments. A substantial proportion of the epilimnetic bottom area is however covered by the moss *Fontinalis* sp., which was not contained in the sampled cores. It is therefore likely that the epilimnetic sediments in Klintsjön in fact take up CO_2 from the water. It has been shown that benthic primary production can be substantial in clear-water lakes (Hargrave 1969; Björk-Ramberg and Ånell 1985), and therefore it is plausible to assume that the epilimnetic sediments constitute a significant sink of CO_2 in Klintsjön.

The humic lake Skärshultsjön (Figure 6b) emits CO_2 to the atmosphere during summer stratification (range 128 – 287 mg C m^{-2} d^{-1}; mean 218 ± 40 mg C m^{-2} d^{-1}). Plankton respiration is the dominant source of CO_2 in the epilimnetic water-column (158 ± 27 mg C m^{-2} d^{-1}), while photo-oxidation contributes only 25 ± 6 mg C m^{-2} d^{-1}. Epilimnetic sediments release 64 ± 5 mg C m^{-2} d^{-1} to the water, while respiration in hypolimnetic sediments frees 27 ± 3 mg C m^{-2} d^{-1}. The estimate of epilimnetic sediment respiration can be considered robust, as soft bottoms dominate in Skärshultsjön, and the highly stained water limits benthic primary production.

Several interesting patterns can be seen when comparing the in-lake carbon cycling in these two lakes. As discussed before, net plankton respiration is the dominating CO_2 producer in both lakes. While photo-oxidation is important in Klintsjön, it is rather insignificant in Skärshultsjön. Further, while epilimnetic sediments probably are sinks of CO_2 in Klintsjön, they clearly are sources of CO_2 in Skärshultsjön.

a) Klintsjön (clear-water)

CO_2

48 ± 23
$(-18 - +87)$

UV

CO_2

61 ± 25

DOC

PR
87 ± 49

?

7 ± 2

26 ± 6

b) Skärshultsjön (humic)

CO_2

218 ± 40
$(+128 - +287)$

UV

CO_2

25 ± 6

DOC

PR
158 ± 27

64 ± 5
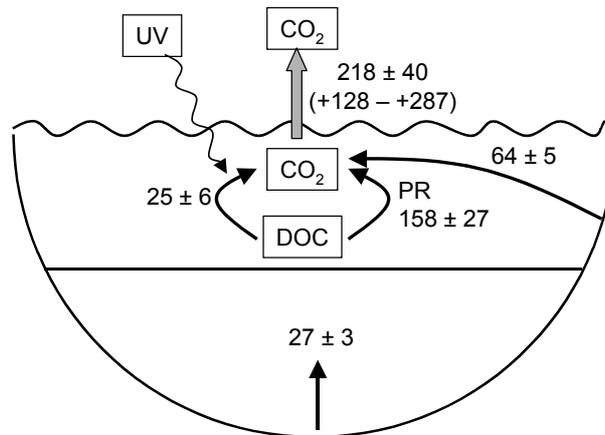
27 ± 3

Figure 6. CO_2 fluxes in a) Klintsjön and b) Skärshultsjön during summer stratification. All values are given as mg C m^{-2} d^{-1} $\pm$ standard error. PR is net plankton respiration. Atmospheric flux is an average value based on one measurement each summer from 2000 to 2003; the numbers in parentheses give the range. Sediment fluxes are expressed per area lake surface.

This difference can be attributed to the stimulation of sediment respiration by allochthonous organic carbon (Figure 3; Paper III) on one hand, and to the difference in water transparency on the other hand. Regarding the magnitude of CO_2 fluxes in both lakes (Figure 6), it is evident that in-lake processes can account for the CO_2 flux between the lakes and the atmosphere, while the import of CO_2 to the lakes with surface and groundwater is probably of variable and episodic importance.

Two features are surprisingly similar in the two lakes. First, hypolimnetic sediment respiration is almost identical in the two lakes, and comparatively low compared to fluxes in the epilimnia. Thus, even if hypolimnetic sediments are included, plankton respiration is still the dominating source of CO_2 in both lakes. Second, the atmospheric CO_2 balance of the two lakes displayed considerable variation. For Klintsjön, this implies that the lake is shifting between being a sink and a source of atmospheric CO_2, while Skärshultsjön is merely shifting the extent of CO_2 emission. Since the CO_2 emitted from the lakes is largely produced by in-lake microbial metabolism, this variability indicates substantial shifts in the metabolic balance (Jansson et al. 2000). For example, the lowest CO_2 emission for Skärshultsjön was accompanied by a bloom of the phytoplankton *Gonyostomum semen* in the lake (personal observation). Metabolic as well as abiotic processes are affected by weather conditions; solar irradiation affects both the extent of photosynthesis and photo-oxidation, and increased run-off after heavy rains implies both high terrestrial export of DOC (Hinton et al. 1997) and a higher potential for surface water and groundwater-mediated imports of CO_2. Thus, weather clearly is a major trigger of variability in the CO_2 balance of individual lakes.

The patterns described so far refer to the summer situation, but they may to a certain degree be applicable to other seasons as well. Photo-oxidation is certainly most important in summer, when solar irradiation is at its yearly maximum. Thus, the contribution of photo-oxidation during other seasons will probably be less important. The relative contribution of plankton and sediment respiration during other seasons is more difficult to predict. Both processes are similarly affected by substrate supply (Figure 3) and temperature (Bergström and Salonen 1979; White et al. 1991). Temperatures in the water and in the sediment co-vary in the upper mixed layer, and can therefore not be expected to affect the relative importance of sediment and plankton respiration. It can however be hypothesized that during winter, when substrate supply to the water-column is low due to low water flows, continued mineralization of previously deposited organic carbon in the sediments will increase the importance of sediment respiration compared to plankton respiration. During spring and autumn, inflowing water will supply plankton with new substrate, but on the other hand, also the deep sediments will contribute to mixed-layer CO_2 production. The contribution of sediment and plankton respiration to whole-lake mineralization during spring and autumn

might therefore largely resemble the summer situation. Thus, the patterns delineated in Figure 6 may be fairly representative for the open-water seasons.

Conclusions and Perspectives

In summary, this thesis arrives at the following major results:

1. Swedish boreal lakes are generally supersaturated in CO_2 with respect to the atmosphere. Lake pCO_2 is mainly a function of the humic content, indicating that allochthonous organic carbon fuels respiration in these lakes.

2. Most of the CO_2 emitted from boreal Swedish lakes is derived from respiration by the plankton community. The contribution of photo-oxidation is limited, but may at times be important in clear-water lakes. Sediment respiration contributes with roughly 10% to the CO_2 emission from boreal and subarctic lakes.

3. CO_2 emission is a major carbon loss factor in boreal lakes. Between 30 and 80% of the organic carbon exported from terrestrial soils are lost during passage through lakes and rivers. Carbon budgets of the boreal landscape should therefore account for CO_2 emission from lakes.

4. The pCO_2 of global lakes is largely independent of temperature, while the DOC concentration explains significant variation in lake pCO_2. Climate change will therefore affect the pCO_2 of lakes not primarily by increased temperature, but rather by changes in the export of DOC from terrestrial soils to lakes. Regarding the current and predicted trend towards higher terrestrial DOC export in large parts of Sweden, there probably is a corresponding trend of increasing CO_2 emission from Swedish boreal lakes.

The present thesis not only provides further evidence that lakes are disproportionately important sites of carbon cycling, but also substantiates the concept that net heterotrophic ecosystem metabolism is the major source of CO_2 in lakes. Furthermore, the thesis presents the first prediction of the possible feedback of lake CO_2 emission to climate change. Describing the mechanisms, importance and feedback of lake CO_2 emission, this thesis represents a considerable step towards the integration of freshwaters in models of the global carbon cycle.

However, the concept of freshwaters being globally significant sites of carbon cycling is almost exclusively based on data from the northern temperate and boreal zone. As global science needs global data, future research should focus on so-far neglected, freshwater-rich areas in the tropics and the

southern hemisphere. In the ambition to integrate freshwaters in the global carbon cycle, the need for truly global data is imperative.

Also, several aspects of carbon cycling in freshwaters are still poorly understood. For example, organic carbon is so far mostly treated as a black box, while qualitative aspects may be decisive for its fate in the environment. Furthermore, the significant carbon sink in lake sediments has been addressed by very few studies, and deserves more attention. Lastly, future studies should to a larger degree integrate terrestrial and aquatic carbon fluxes, in order to provide landscape-scale assessments of carbon cycling. In our changing world, knowledge of carbon cycling is essential in order to prepare society for the challenges of future climate conditions.

Sammanfattning (Summary in Swedish)

Allt liv på jorden är baserat på ämnet kol. Gröna växter tar upp koldioxid ur luften, och omvandlar det till organisk kol (t ex trä, blad, rötter). Vi människor, men även alla djur, svampar och många bakterier, livnär oss på det organiska kol som växterna har producerat, och när vi sedan andas ut avger vi koldioxid till luften igen. Kol ingår dock inte bara i biologiska utan även i geologiska processer. Koldioxid löser sig och lagras i havsvatten, vulkanutbrott frigör koldioxid, och det organiska kolet i alger som sjunker till havsbotten blir till olja efter några miljoner år. På så sätt hänger allt liv på jorden och jorden själv ihop i ett kolkretslopp.

Människan ingriper i kolkretsloppet genom att elda upp fossila bränslen (olja, kol, naturgas), vilket frigör koldioxid som har varit borta ur kretsloppet sedan miljontals år. Detta har lett till att koldioxidhalten i atmosfären har stigit. Eftersom koldioxid är en växthusgas, som kan hålla kvar värme i atmosfären, har de ökande halterna medfört att jordens klimat har blivit varmare de senaste deciennerna. Denna trend kommer med all sannolikhet att hålla i sig, med betydande förändringar av jordens klimat till följd.

För att förstå männsikans inverkan på kolkretsloppet och dess påverkan på klimatet, måste vi ha kunskap om det naturliga, ostörda kolkretsloppet. Stora delar av kolkretsloppet är dock fortfarande otillräckligt kända. Bland annat är inlandsvattnens roll i kolkretsloppet till stora delar okänt, men det finns studier som pekar på att sjöar och älvar är mycket viktigare än man hittills har trott.

I min avhandling undersöker jag vilken roll sjöar spelar i det svenska skogslandskapets kolkretslopp. Eftersom det norra barrskogsbältet täcker en stor del av Sveriges yta, och 10% av jordens landyta, har resultaten stor betydelse både på ett nationellt och på ett globalt plan.

Det visade sig att nästan alla skogssjöar avger koldioxid till atmosfären. Koldioxid bildas i en sjö när bakterier, som förekommer naturligt i sjövatten, tillgodogör sig löst organiskt kol i form av humusämnen, som har sköljts från omkringliggande mark till sjön. Sjöar med en hög halt av humusämnen, som känns igen på vattnets mörka färg, har därför en högre halt av koldioxid än klara, humusfattiga sjöar. Även solens UV-strålning kan bryta ner humusämnen till koldioxid, men denna process visade sig vara av mindre betydelse för sjöns koldioxidhalt. Dessutom visar resultaten att den mesta koldioxiden produceras av bakterier som lever i själva vattnet, medan bakterier som lever på sjöbotten bidrar med en mindre andel.

Koldioxidemission från sjöar är en betydande faktor i det svenska skogs-landskapets kolomsättning. Ungefär hälften (mellan 30 och 80%) av alla humusämnen som sköljs från mark till sjöar och vattendrag blir omvandlade till koldioxid och avges sedan till atmosfären, innan vattnet når havet. Visserligen är upptaget av koldioxid genom skogens alla träd mycket större än sjöarnas koldioxidemission, men det gäller att tänka långsiktigt. I det långa loppet (mer än 100 år) kommer de flesta träd och skogsprodukter att förbrännas eller ruttna bort, och koldioxiden som träden tog upp kommer således att släppas ut igen. Därför ska sjöarnas koldioxidemission snarare jämföras med skogens långsiktiga lagring av organiskt kol, som sker i marken. Denna lagring av organiskt kol i skogens mark är i ungefär samma storlek som emissionen av koldioxid från skogens sjöar. Detta innebär att man överskattar skogslandskapets totala koldioxidupptag om man inte tar hänsyn till sjöarnas koldioxidemission.

Vidare fann jag att klimatförändringen kommer att påverka emissionen av koldioxid från sjöar. Klimatförändringen kommer att medföra ändrad nederbörd, vilket i sin tur betyder att transporten av humusämnen från mark till sjöar och vattendrag kommer att påverkas. Den ändrade tillförseln av humus till sjöar kommer att resultera i motsvarande förändringar i sjöars koldioxidhalt, medan en högre vattentemperatur i sig inte kommer att ha någon större effekt. Under de senaste deciennerna har en tilltagande humushalt i många svenska sjöar och vattendrag observerats, och denna trend kommer med stor sannolikhet att fortsätta i stora delar av landet. Således är det troligt att koldioxidemission från svenska sjöar har ökat de senaste deciennerna, och kommer att fortsätta att öka i framtiden.

Den som vill veta mer hänvisas till min artikel i tidskriften Forskning och Framsteg, som kommer att publiceras inom kort.

Zusammenfassung (Summary in German)

Kohlenstoff ist ein Hauptbestandteil aller Lebewesen. Grüne Pflanzen nehmen Kohlendioxid aus der Luft auf, und wandeln es mit Hilfe von Sonnenenergie in organischen Kohlenstoff (z.B. Holz und Blätter) um. Wir Menschen, alle Tiere, Pilze und viele Bakterien ernähren uns vom organischen Kohlenstoff, den die Pflanzen produzieren, und atmen das dabei entstehende Kohlendioxid wieder aus. Aber Kohlenstoff ist nicht nur Teil von biologischen, sondern auch geologischen Prozessen. Kohlendioxid löst sich im Meerwasser und wird dort gelagert, Vulkanausbrüche setzen Kohlendioxid frei, und der organische Kohlenstoff in Algen, die auf den Meeresboden sinken, wird im Laufe von Jahrmillionen zu Erdöl. Auf diese Weise sind alle Lebewesen und die Erde durch den Kohlenstoffkreislauf verbunden.

Wir Menschen verändern den natürlichen Kohlenstoffkreislauf durch die Verbrennung fossiler Brennstoffe (Erdöl, Kohle, Erdgas). Dadurch wird Kohlenstoff freigesetzt, der vor Jahrmillionen aus dem Kreislauf verschwand. Das hat dazu geführt, daß der Kohlendioxidgehalt der Athmosphäre angestiegen ist. Weil Kohlendioxid ein Treibhausgas ist, das Wärme in der Athmosphäre zurückhalten kann, hat der steigende Kohlendioxidgehalt eine merkbare Klimaerwärmung während der letzten Jahrzehnte zur Folge gehabt.

Um den menschlichen Eingriff in den Kohlenstoffkreislauf und die damit zusammenhängende Klimaerwärmung verstehen zu können, brauchen wir Kenntnisse über den natürlichen, ungestörten Kohlenstoffkreislauf. Viele Teile des Kohlenstoffkreislaufes sind aber noch unzureichend erforscht. Unter anderem wissen wir nur wenig über die Rolle von Seen und Flüssen. Weil Süßgewässer weniger als 1% der Erdoberfläche bedecken, hat man bisher angenommen, daß sie eine unbedeutende Rolle im Kohlenstoffkreislauf spielen. Es gibt aber Studien, die zeigen, daß Kohlenstoffumsetzung in Süßgewässern weit wichtiger sein kann als bisher angenommen.

In meiner Doktorarbeit untersuche ich die Rolle von Seen im Kohlenstoffkreislauf der schwedischen Nadelwaldzone. Ungefähr die Hälfte Schwedens ist von Nadelwald bedeckt, und ein Großteil der ungefähr 100 000 schwedischen Seen liegt in der Nadelwaldzone. Weil die nördliche Nadelwaldzone außerdem rund 10% der gesamten Erdoberfläche ausmacht, sind die Resultate meiner Arbeit nicht nur fuer den Kohlenstoffkreislauf Schwedens, sondern auch der ganzen Erde von Bedeutung.

Es zeigte sich, daß so gut wie alle schwedischen Waldseen Kohlendioxid an die Athmosphäre abgeben. Das Kohlendioxid wird von Bakterien produziert, die natürlich in Seen vorkommen. Die Bakterien ernähren sich von organischem Kohlenstoff in der Form von Humusstoffen, die vom Waldboden in die Seen gespült werden, und atmen dabei Kohlendioxid aus. Humusreiche Braunwasserseen haben deswegen einen höheren Kohlendioxidgehalt als humusarme Klarwasserseen. Auch die UV-Strahlung der Sonne kann Humusstoffe in Kohlendioxid verwandeln, aber dieser Prozess ist von geringerer Bedeutung als bakterieller Humusabbau. Darüberhinaus zeigte sich, daß der Großteil des Kohlendioxids von Bakterien produziert wird, die im freien Wasser leben, während Bakterien im Seeboden nur einen geringen Beitrag zum Kohlendioxidgehalt eines Sees liefern.

Die Kohlendioxidemission von Seen ist ein wichtiger Faktor im Kohlenstoffkreislauf des schwedischen Nadelwaldes. Ungefähr die Hälfte (zwischen 30 und 80%) aller Humusstoffe, die aus den Böden in Seen und Flüsse gespült werden, werden in Seen zu Kohlendioxid verwandelt und in die Athmosphäre abgegeben, bevor sie das Meer erreichen. Zwar ist die Kohlendioxidaufnahme aller Bäume um ein Vielfaches größer als die Kohlendioxidemission der Seen, aber über einen längeren Zeitraum gesehen (über 100 Jahre) werden die meisten Bäume und Waldprodukte verrotten oder verbrannt werden, und damit wird das Kohlendioxid wieder freigesetzt. Deswegen muss die Kohlendioxidemission von Seen mit der langfristigen Lagerung von organischem Kohlenstoff, die in Waldböden erfolgt, verglichen werden. Diese Lagerung von organischem Kohlenstoff in Waldböden ist in derselben Größenordnung wie die Kohlendioxidemission der Waldseen. Folglich ist die Kohlendioxidaufnahme der Nadelwaldzone bislang überschätzt worden, weil die Kohlendioxidemission von Seen nicht berücksichtigt worden ist.

Die gegenwärtige Klimaveränderung wird die Kohlendioxidemission von Seen verändern. Durch die Klimaveränderung wird sich der Niederschlag ändern, und dadurch der Transport von Humusstoffen von Böden zu Gewässern. Die veränderte Humuszufuhr zu Seen wird zu entspechend veränderten Kohlendioxidgehalten in Seen führen, während eine höhere Wassertemperatur vermutlich keinen größeren Effekt haben wird. Während der letzten Jahrzehnte konnte in vielen schwedischen Seen und Flüssen ein steigender Gehalt an Humusstoffen beobachtet werden, und dieser Trend wird sich aller Wahrscheinlichkeit nach in einem Großteil des Landes fortsetzten. Damit ist anzunehmen, daß die Kohlendioxidemission von schwedischen Seen während der letzten Jahrzehnte gestiegen ist, und daß sie in Zukunft weiter ansteigen wird.

Thanks / Danke / Tack

Many people contributed to this work, and given my rather fragmentary memory, I'll probably forget to mention some of you. So, if you feel you should be mentioned here but you aren't, rest assured that I will be thankful to you anyway!

Lars, well, how could I forget to thank you! I honestly could not imagine a better supervisor than you are: an excellent scientist, enthusiastic and supportive, but still giving me the freedom to choose my own directions (at least that was my perception!). Above all, you are "schysst" as well. The only thing I missed was a slightly more genuine interest in sports…

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