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

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Dissertation presented at Uppsala University to be publicly examined in Ekmansalen, Kärnhuset, EBC, Uppsala, Friday, October 14, 2005 at 10:00 for the degree of Doctor of Philosophy. The examination will be conducted in English.

Abstract


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 CO₂ with respect to the atmosphere, resulting in an emission of CO₂ from lakes to the atmosphere. Lake pCO₂ 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 CO₂. This conclusion is supported by independent field studies, showing that net plankton respiration accounts for most of the CO₂ emitted from Swedish boreal lakes, while photochemical mineralization and sediment respiration were less important.

Mineralization of terrigenous DOC and subsequent emission of CO₂ 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 CO₂ 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 pCO₂ 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 CO₂ 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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ISSN 1651-6214
ISBN 91-554-6329-0
urn:nbn:se:uu:diva-5920 (http://urn.kb.se/resolve?urn=nbn:se:uu:diva-5920)
Der Ball ist rund
Sepp Herberger
List of Papers


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Abbreviations

CH₄     Methane
CO₂     Carbon dioxide
DIC     Dissolved inorganic carbon
DOC     Dissolved organic carbon
pCO₂    Partial pressure of carbon dioxide
Pg      Petagram, 10¹⁵ 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 CO₂ 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 (CH₄) to the atmosphere than the ocean, corresponding to 6-16% of all natural CH₄ sources. In a regional study of the Amazon basin, emission of CO₂ 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 CO₂ supersaturation in lakes.

Sources and sinks of CO₂ in lakes

The majority of the world’s lakes are supersaturated in CO₂ with respect to the atmosphere, and consequently emit CO₂ to the atmosphere (Cole et al. 1994). The emission of excess CO₂ from lakes may be sustained by several processes, both biotic and abiotic (Figure 1).

CO₂ 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 CO₂, and may therefore be significant sources of CO₂ to lakes. Accordingly, Jones et al. (2001) reported that roughly 75% of the CO₂ emitted from Loch Ness in Scotland can be attributed to riverine inputs of CO₂ derived from soil respiration. On the other hand, Jonsson et al. (2001) found that import of CO₂ with surface water in-
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 CO₂ 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 CO₂ is therefore undoubtedly important in some cases, but it can probably not account for the consistently observed CO₂ supersaturation in lakes (Hanson et al. 2003).

Another abiotic source of CO₂ 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 CO₂ (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 CO₂ in some lakes, its general importance for the overall mineralization of DOC in lakes is not well constrained.

Finally, CO₂ 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 CO₂ (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 CO₂ (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
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 pCO₂ in the water, lake pCO₂ is the main driver of CO₂ flux between boreal lakes and the atmosphere.

For determination of the partial pressure of carbon dioxide (pCO₂) 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 pCO₂ 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 CO₂ (pCO₂) 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 pCO₂ for each sampling occasion. The pCO₂ of ambient air, which was used for equilibration, was measured at each sampling occasion. From the sample measurements we calculated pCO₂ in the water via Henry’s constant according to Weiss (1974) after corrections for atmospheric pressure and for the amount of CO₂ added to the bottles with headspace air.

Mineralization rates in water and sediments

This thesis presents mineralization rates by plankton respiration, photodissimilation 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 pCO₂ in lake water by infrared gas analysis. As the CO₂ produced by mineralization readily reacts with water to form carbonic acid, we measured CO₂ as dissolved inorganic carbon (DIC), i.e. the sum of free CO₂, H₂CO₃, HCO₃⁻ and CO₃²⁻. For the sediment study, we also measured methane (CH₄), 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 CO₂. 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 CO₂) and a flame ionisation detector (for CH₄). The pCO₂ and pCH₄ 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 CH₄ during incubation.
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
pCO₂, we conclude that bacterial utilization of DOC as a substrate (Tranvik 1988) is the major process behind the correlation between DOC and pCO₂. Thus, the consistent supersaturation of CO₂ 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 CO₂ 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 pCO₂ 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 CO₂ in boreal lakes
Papers II and III

Results from Papers II and III indicate that plankton respiration is the most important source of CO₂ 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
lake (14%). Thus, net plankton respiration was a more important contributor to lake CO₂ 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 CO₂ 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 CO₂ 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 CO₂ and CH₄. Mean sediment respiration was calculated for the sediments that are in contact with the upper mixed layer. Both mean sediment respiration rate and CO₂ 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 CO₂ 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. CO₂ consumption, which we ascribe to benthic primary production on the illuminated lake bottoms. Still, all clear-water lakes apart from one emitted CO₂ to the atmosphere. Hence, we can conclude that processes in the water-column contribute more to the exchange of CO₂ 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 CO₂ 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 CO₂+CH₄ 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.

CO₂ emission from lakes – does it matter?

Paper IV

We found that CO₂ 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 pCO₂ and DOC (Figure 2) in order to predict CO₂ emission for all lakes in 21 major catchments in boreal Sweden. Lake CO₂ 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 km² and contain 79 536 lakes:

\[
\text{TOC}_\text{export} = \text{TOC}_\text{sea} + S + E_L + E_R \quad (1)
\]

\(\text{TOC}_\text{export}\) is the export of total organic carbon (TOC, which consists to over 90% of DOC) from terrestrial soils to freshwaters, \(\text{TOC}_\text{sea}\) is the riverine export of TOC to the sea, \(S\) is permanent sedimentation of organic carbon, \(E_L\) is the CO₂ emission from lakes, and \(E_R\) is the CO₂ 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 pCO₂. Then, we used data
from the Swedish lake register (www.smhi.se) and from the Swedish na-
tional lake inventory (www.ma.slu.se) in order to estimate CO₂ emission
from all 79,536 lakes. 2120 lakes within the catchments are part of the na-
tional lake inventory, and for these lakes we could estimate pCO₂ from the
TOC concentration. From pCO₂, we calculated the CO₂ 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 CO₂ emission and sur-
face area of the 2120 inventory lakes with the lake register, we could calcu-
late the average CO₂ emission for each size class. Multiplication with the
total lake surface area covered by each size class in each catchment finally
returned the total CO₂ emission of lakes in each catchment (Eₐ). In order to
calculate the annual emission of CO₂, we accounted for the accumulation of
CO₂ during ice cover, and the subsequent emission of CO₂ during ice melt.

The emission of CO₂ from rivers (Eᵣ) was estimated from the area-
weighted mean CO₂ emission from all lakes in the catchment, times the area
covered by running water in each catchment. As rivers frequently have
higher pCO₂ than lakes (Cole and Caraco 2001), our estimate of Eᵣ is con-
servative. 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 (TOCₗ) was calculated
from surveyed TOC concentration at the river mouths (www.ma.slu.se) and
discharge (www.smhi.se).

We found that lake CO₂ emission was a major organic carbon loss factor
in the 21 boreal catchments. Averaged for all catchments, lake CO₂ emission
was about eight times higher than both organic carbon burial in sediments
and CO₂ emission from rivers, and was roughly equal to riverine organic
carbon export to the sea. Total loss of TOC in lakes (CO₂ emission + sedi-
mentation) 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 CO₂ 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 resi-
dence 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 (CO₂ 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 CO₂ emission for the carbon balance of the boreal landscape depends primarily on the CO₂ balance of the forest. Net CO₂ uptake by boreal forests is typically two orders of magnitude higher than CO₂ 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 CO₂ 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 CO₂ that is accumulated in forest soils. Typical carbon accumulation rates in boreal forest soils are in the same order of magnitude as lake CO₂ 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), CO₂ emission from lakes significantly affects the carbon balance of the boreal landscape. Furthermore, Valentini et al. (2000) showed that the net CO₂ uptake of forests decreases with increasing latitude, and may even be turned into a net CO₂ 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 CO₂ between the boreal landscape and the atmosphere.
How will climate change affect the CO2 emission from lakes?

In order to assess the possible feedback of lake CO2 emission to climate change, we analyzed pCO2 in a large set of globally distributed lakes. From the results of this study, we predict that the CO2 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 \textit{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 pCO2 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 pCO2 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 pCO2.

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 pCO2 from 4902 global lakes, which is the so far largest collection of pCO2 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 pCO2. 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 CO2 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 pCO2 in lakes than is temperature. Both annual mean air temperature and in-situ water temperature explained very little of the variation in pCO2 (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 pCO2 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 pCO₂ against a) mean annual air temperature ($y=2.95+0.012\times x$, $p<0.0001$, $R^2=0.06$) b) in-situ water temperature at the time of sampling ($y=2.96+0.004\times x$, $p<0.001$, $R^2=0.003$), and c) DOC concentration ($y=2.67+0.414\times x$, $p<0.0001$, $R^2=0.26$). 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\textsubscript{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\textsubscript{2} to the atmosphere. Based on one measurement each summer from 2000 to 2003, the atmospheric flux of CO\textsubscript{2} ranged between $-18$ (uptake) and $+83$ (emission) mg C m$^{-2}$ d$^{-1}$. On average however, Klintsjön emitted CO\textsubscript{2} to the atmosphere ($48 \pm 23$ mg C m$^{-2}$ d$^{-1}$; mean $\pm$ standard error). In the epilimnetic water-column, $61 \pm 25$ mg C m$^{-2}$ d$^{-1}$ were produced by photo-oxidation, and $87 \pm 49$ 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 $7 \pm 2$ mg C m$^{-2}$ d$^{-1}$, and hypolimnetic sediments released $26 \pm 6$ 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\textsubscript{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\textsubscript{2} in Klintsjön.

The humic lake Skärshultsjön (Figure 6b) emits CO\textsubscript{2} to the atmosphere during summer stratification (range $128 - 287$ mg C m$^{-2}$ d$^{-1}$; mean $218 \pm 40$ mg C m$^{-2}$ d$^{-1}$). Plankton respiration is the dominant source of CO\textsubscript{2} in the epilimnetic water-column ($158 \pm 27$ mg C m$^{-2}$ d$^{-1}$), while photo-oxidation contributes only $25 \pm 6$ mg C m$^{-2}$ d$^{-1}$. Epilimnetic sediments release $64 \pm 5$ mg C m$^{-2}$ d$^{-1}$ to the water, while respiration in hypolimnetic sediments frees $27 \pm 3$ 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\textsubscript{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\textsubscript{2} in Klintsjön, they clearly are sources of CO\textsubscript{2} in Skärshultsjön.
Figure 6. CO₂ fluxes in a) Klintsjön and b) Skärshultsjön during summer stratification. All values are given as mg C m⁻² d⁻¹ ± 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 CO₂ with respect to the atmosphere. Lake pCO₂ is mainly a function of the humic content, indicating that allochthonous organic carbon fuels respiration in these lakes.

2. Most of the CO₂ 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 CO₂ emission from boreal and subarctic lakes.

3. CO₂ 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 CO₂ emission from lakes.

4. The pCO₂ of global lakes is largely independent of temperature, while the DOC concentration explains significant variation in lake pCO₂. Climate change will therefore affect the pCO₂ 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 CO₂ 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 CO₂ in lakes. Furthermore, the thesis presents the first prediction of the possible feedback of lake CO₂ emission to climate change. Describing the mechanisms, importance and feedback of lake CO₂ 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)


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 decennerna. Denna trend kommer med all sannolikhet att hålla i sig, med betydande förändringar av jordens klimat till följd.

För att förstå människans 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 koldioxid 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 skogslandskapets kolomsättning. Ungefär halften (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 leppet (mer än 100 år) kommer de flesta träd och skogsprodukter att förbrännas eller ruttna bort, och koldioxiden som träderna 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 decennerna 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 decennerna, 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.


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 Atmosphäre abgegeben, bevor sie das Meer erreichen. Zwar ist die Kohlendioxidemission von 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 Kohlendioxidemission von Seen nicht berücksichtigt worden, weil die Kohlendioxidemission von Seen nicht berücksichtigt worden ist.

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…

Mats, you were a distant co-advisor, but I really appreciate your insightful thinking and constructive comments on manuscripts. You gave the word “klurig” a deeper meaning.

Grete, thanks for everything! It was great to work so closely together with you. Anki, thank you for demonstrating that it is possible to be a laid-back and excellent scientist. Anders i Abisko, thanks for your help to get things started in the beginning. David, thanks for invaluable lessons about gases, for a nice field trip, and great discussions!

There is a bunch of people at the Limnology Department in Uppsala who deserve special attention. Anders Broberg, you were the first contact I got with Uppsala, and the first impression still holds. Thank you for being such a nice guy, for good company during teaching, and all the peanuts and red wine! Peter Blomqvist, I miss you! You were truly inspiring and encouraging, and in a way you still are. Janne, you are a hero! What else is there to say? Stefan, Staffan and Monica, thanks for help with any kinds of technical problems. Sofi, Erika, Eddie and Kristiina, thanks for great help with field, lab, and computer work. Silke, my everlasting roommate and fellow German, thanks for nice chats and a good time. Marcus, Anna and Anders, thank you for employing me while I was a hang-around. Thanks to the Ethiopian connection (Yosef, Elias, Zinabu, Girma) for widening my horizon and your delightful sense of humor. All you other limnos, thanks for your great company during the last eight years, and thanks for making this a great place to work.

in Deutschland, die mich während des langen schwedischen Exils nicht vergessen haben.

Ett stort tack till min svenska familj för att ni har blivit min svenska familj. Tack alla kompisar och fotbollspolare för oräkneligt många roliga timmar. Tack också till Birger i Malingsbo för kaffe och kaka, och till Roland för hjälp i Aneboda.

Slutligen, Anna... du är navet i mitt liv. Tack för all glädje! Vi har haft fantastiska år tillsammans, och jag ser fram emot många fler. Und Liv, dieses kleine Buch ist nun also das Ergebnis all der Male, an denen ich zu dir gesagt habe: „Papa fährt jetzt zur Arbeit“ oder „Papa sitzt am Computer und arbeitet“. Wenn du das verstehen könntest, würdest du lachen, und ich mit dir.
References


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