Climate-dependent CO₂ emissions from lakes

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Inland waters, just as the world’s oceans, play an important role in the global carbon cycle. While lakes and reservoirs typically emit CO₂, they also bury carbon in their sediment. The net CO₂ emission is largely the result of the decomposition or preservation of terrestrially supplied carbon. What regulates the balance between CO₂ emission and carbon burial is not known, but climate change and temperature have been hypothesized to influence both processes. We analyzed patterns in carbon dioxide partial pressure (pCO₂) in 83 shallow lakes over a large climatic gradient in South America and found a strong, positive correlation with temperature. The higher pCO₂ in warmer lakes may be caused by a higher, temperature-dependent mineralization of organic carbon. This pattern suggests that cool lakes may start to emit more CO₂ when they warm up because of climate change.


1. Introduction

The importance of the world’s oceans in global carbon cycling is well known and their influence on atmospheric CO₂ concentrations is explicitly incorporated in climate change models [Intergovernmental Panel on Climate Change (IPCC), 2007]. So far, however, the role of inland waters has received less attention even though recent studies indicate that they play an important role in regulating carbon fluxes as well [Cole et al., 2007; Downing et al., 2008; Duarte et al., 2008]. A significant part of the organic carbon initially sequestered as CO₂ by terrestrial ecosystems ends up in rivers and lakes. Only about half of this carbon is transported to the oceans [Cole et al., 2007]. Much of the terrestrially produced carbon entering inland waters is buried in sediments or emitted as CO₂ to the atmosphere [Cole et al., 2007]. In addition, primary production within inland waters represents a substantial carbon flux, especially in lakes with high concentrations of nutrients allowing high productivity [Williamson et al., 2009]. This turns inland waters into carbon processing hot spots in terrestrial landscapes and despite the fact that inland waters occupy a relatively small fraction of the Earth’s surface, they play an important role in the global carbon cycle by processing large amounts of terrestrially derived carbon [Battin et al., 2009]. Depending on the balance between processes such as respiration, primary production, groundwater carbon inflow and calcite precipitation, these systems may be carbon sinks, or become supersaturated with CO₂ and act as CO₂ sources to the atmosphere [Cole et al., 1994, 2000; Duarte and Prairie, 2005; Sobek et al., 2005]. All these processes are likely sensitive to changes in temperature and hydrology.

Very little is known about the overall effects of climatic change on the carbon cycling in inland waters. Temperature, for example, may affect carbon cycles in a direct way through its influence on aquatic respiration [Sand-Jensen et al., 2007] and primary production [Planagan et al., 2003], which may be most evident when it coincides with an increase in nutrient loading [Christoffersen et al., 2006]. A differential temperature dependence of respiration and photosynthesis may lead to a decrease in carbon fixation and an increase in carbon emission [Lopez-Urrutia et al., 2006]. Altered precipitation regimes may influence lakes’ metabolism as well. For instance through its effect on the hydraulic residence time, which can have several effects including altering carbon sedimentation and mineralization [Algesten et al., 2004; Curtis, 1998]; changing terrestrial inputs of nutrients and organic matter, and possibly primary production as well [Reynolds, 1994; Schallenber and Burns, 1997]. Temperature and precipitation also have an indirect effect on lake’s carbon cycle through their influence on terrestrial carbon fixation and the subsequent carbon leaching to the lake [Sobek et al., 2005].
2. Methods

2.1. Site Description

[5] We sampled 82 lakes in the East of South America (Figure 1). Lakes were selected to resemble each other as much as possible morphologically, but to vary as much as possible in climate and, within climate regions, in trophic state. The lakes in our data set ranged from being oligotrophic to hypertrophic (Table 1). All lakes were shallow (maximum mean depth 4.5 m) and relatively small (surface area ranged between 0.09 and 2.53 km²) (Table 1). The climate conditions at the sampling sites varied considerably; the most northern lake sites had maximum monthly air temperature up to 28.7°C whereas at the most southern lake locations the maximum was only 8.2°C [New et al., 2002]. At the time of sampling the lake water temperature ranged from approximately 10 to 30°C. In each climate region, lakes were selected to vary as much as possible in trophic state (Table 1 and Kosten et al. [2009a]).

2.2. Sampling

[6] Lakes South of 25°S were sampled once during summer, the lakes nearer to the equator were sampled during dry season between November 2004 and March 2006.

[7] We collected water samples along the whole water column with a 1.5 m long tube at 20 random points in each lake between 0930 and 1200 LT. Two liters of each of these depth-integrated samples were gathered in a 40 L bucket resulting in a depth and area integrated bulk sample. Filtration for various analyses in the laboratory was conducted directly after collection. Water and filters were then frozen until analysis. Sediment samples of the top 2 cm were taken in the center of the lake with a Kajak corer.

[8] Annual mean precipitation data were obtained from a high-resolution data set of surface climate over global land areas [New et al., 2002].

2.3. Sample Analysis

[9] We determined the acid neutralizing capacity (ANC) titrimetrically using 0.05N HCl on unfiltered samples in the field directly after sampling. pH was determined also on unfiltered samples using a probe. Chlorophyll a (chl a) was extracted from filters (GF/C S&S) with 96% ethanol and absorbance was measured at 665 and 750 nm [Musch, 1980]. For dissolved organic carbon, (DOC) analysis water was filtered through GF/F Whatman filters. DOC was determined by a Total Organic Carbon analyzer (Model 700, O.I.C International BV). As a measure for humic substances spectrophotometric light absorption at 380 nm was measured [Butteveld, 1995] in filtered (0.45 μm S&S) water. The concentration of organic N and C in sediment was determined, after carbonate removal, using a CNS analyzer (NA-1500).

[10] The δ²H and δ¹⁸O of the bulk lake water sample were determined in a Multiflow system connected to an Isoprime Mass Spectrometer (Thermo Electron, Waltham, Massachusetts, United States). All isotopic ratios are expressed in δ units relative to the Vienna mean standard ocean water, here as

\[
\delta D \text{ or } \delta ^{18}O = \frac{R_{\text{sample}} - R_{\text{std}}}{R_{\text{std}}} \cdot 1000
\]

in which R_{sample} and R_{std} are δ²H or δ¹⁸O ratios of the sample and standard, respectively. The precision of analysis is ±2.0‰ and ±0.1‰ for δ²H and δ¹⁸O values, respectively.

2.4. Calculations and Data Analysis

[11] The pCO₂ was calculated from the pH and the ANC, adjusting for temperature, ionic strength and air pressure [Cole et al., 1994]. Subsequently, the results were expressed as undersaturated or supersaturated with CO₂ relative to the atmosphere (RS). We used the global average atmospheric CO₂ pressure for the year 2005 as a reference (P. Tans, 2007).

Table 1. General Data on the Lakes Sampled

<table>
<thead>
<tr>
<th></th>
<th>Range</th>
<th>Mean</th>
<th>Median</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (km²)</td>
<td>0.09–2.53</td>
<td>0.62</td>
<td>0.46</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>0.50–4.50</td>
<td>1.80</td>
<td>1.60</td>
</tr>
<tr>
<td>Conductivity (μS cm⁻¹)</td>
<td>38–4930</td>
<td>527</td>
<td>167</td>
</tr>
<tr>
<td>Total nitrogen (mg N L⁻¹)</td>
<td>&lt;0.10–25.80</td>
<td>1.80</td>
<td>0.40</td>
</tr>
<tr>
<td>Total phosphorus (mg P L⁻¹)</td>
<td>0.02–9.14</td>
<td>0.27</td>
<td>0.10</td>
</tr>
<tr>
<td>PVI (%)</td>
<td>0–81</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>Chlorophyll a (µg L⁻¹)</td>
<td>0.6–2889.0</td>
<td>79.66</td>
<td>4.7</td>
</tr>
<tr>
<td>The extinction of light at λ = 380 nm, as a proxy for humic substances (m⁻¹)</td>
<td>0.3–54.2</td>
<td>5.9</td>
<td>4.0</td>
</tr>
<tr>
<td>Total suspended solids (mg L⁻¹)</td>
<td>2–663</td>
<td>43</td>
<td>9</td>
</tr>
<tr>
<td>Light attenuation coefficient (m⁻¹)</td>
<td>0.50–43.60</td>
<td>4.60</td>
<td>2.50</td>
</tr>
</tbody>
</table>

*The percentage of the lake’s volume filled with submerged vegetation.
we derived an inflow:evaporation ratio using Trends in atmospheric carbon dioxide: Recent global CO2, 2009, available at http://www.esrl.noaa.gov/gmd/ccgg/trends/ #global). Lakes were classified as strongly CO2 supersaturated (RS > 1.2); strongly undersaturated (RS < −1.2); or near saturation (−1.2 < RS < 1.2). The percentage of the lake’s volume filled with submerged vegetation (PVI) was determined analogously to Canfield et al. [1984] (for details, see Kosten et al. [2009b]).

As a proxy for the hydrological character of the lake we derived an inflow:evaporation ratio using δ²H and δ¹⁸O of the lake water. The derivation is based on the principle of light isotopes evaporating more quickly than heavy isotopes. The ‘heavier’ the lake water in comparison to the incoming water the more the lake water has been subject to evaporation. We calculated the inflow:evaporation ratio using the Gat-Bowser model [Gat and Bowser, 1991; Rozanski et al., 2001]. The relative humidity input for the model was obtained from a global data set [Bowen and Revenaugh, 2003]. For the stable isotope composition of the inlet water we used the average composition of precipitation at the lake location as a proxy (extracted from map provided by G. J. Bowen (Waterisotopes.org, Purdue University, West Lafayette, 2003, available at http://wateriso.eas.purdue.edu/waterisotopes/pages/data_access/ArcGrids.html) on the basis of data from Bowen and Revenaugh [2003]). However, as the incoming water may have already been subject to evaporation in the watershed before it enters the lake, we may be overestimating the evaporation in the lake. The more the lake was subject to evaporation, for example due to a long hydraulic residence time, the smaller the inflow:evaporation ratio.

Relations of pCO₂ versus climatological variables and local variables were first explored using simple linear regressions. The climatological variables included temperature, mean annual precipitation and the inlet:evaporation ratio. The local variables included PVI, chlorophyll a (chl a), the extinction of light at λ = 380 nm used as a proxy for humic substances (humic), dissolved organic carbon concentration (DOC), and two indicators for the relative influence of aquatic primary production and terrestrial carbon input: (1) the ratio between chlorophyll a and the extinction at λ = 380 nm (chl a: humic); and (2) the ratio between organic carbon and nitrogen in the sediment (C:N). A high chl a: humic ratio indicates that the primary production is relatively large compared to influence of terrestrial organic matter on the lake’s metabolism. To the contrary, a high C:N ratio indicates a relatively strong terrestrial influence on the lake’s metabolism, as the C:N ratio of terrestrial organic matter is generally higher than that of aquatic material [Elser et al., 2000]. Next, we applied multiple linear regressions. The multiple linear regressions modeled pCO₂ using temperature and the variables explaining most of the variance in pCO₂ in the simple linear regressions. To enhance normality, both the dependent and the independent (except for temperature) variables were log transformed before analysis.

All statistical analyses were performed using SPSS for Windows version 15.0 (SPSS, Chicago, Illinois, United States).

### 3. Results

Only in a small fraction (6%) of the lakes, the carbon dioxide partial pressure (pCO₂) was within a range of ±20% from the equilibrium with the atmosphere (near saturation group). Most lakes (80%) were supersaturated (relative saturation > 1.2, Figure 2). The pCO₂ saturation increased with increasing temperature (Table 2). Temperature alone explained 13% (R²) of the variance in pCO₂ (Table 2). Lakes with high abundances of primary producers (either phytoplankton or submerged macrophytes) generally have lower pCO₂’s than expected based on temperature alone.

#### Table 2. Simple Linear Regression Models Describing the Relationship of Lakes’ Partial CO₂ Pressure and Different Climatological and Local Variables

<table>
<thead>
<tr>
<th>Model</th>
<th>Log(pCO₂) =</th>
<th>Regression Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2.08(0.001) + 0.04(0.001) temperature</td>
<td>12.13 0.13 82</td>
</tr>
<tr>
<td>2</td>
<td>0.17(0.877) + 1.08(0.005)</td>
<td>8.37 0.08 82</td>
</tr>
<tr>
<td>3</td>
<td>2.55(0.001) + 0.98(0.001) log(total annual precipitation)</td>
<td>21.87 0.24 70</td>
</tr>
<tr>
<td>4</td>
<td>3.33(0.001) − 0.30(0.001) log(chl a)</td>
<td>18.14 0.19 82</td>
</tr>
<tr>
<td>5</td>
<td>3.15(0.001) − 0.18(0.047) log(PVI)</td>
<td>4.06 0.05 82</td>
</tr>
<tr>
<td>6</td>
<td>3.10(0.001) − 0.08(0.548) log(humic)</td>
<td>0.36 0.01 82</td>
</tr>
<tr>
<td>7</td>
<td>3.50(0.001) − 0.42(0.010) log(DOC)</td>
<td>6.96 0.08 82</td>
</tr>
<tr>
<td>9</td>
<td>3.20(0.001) − 0.36(0.001) log(inflow:evaporation)</td>
<td>21.63 0.21 82</td>
</tr>
<tr>
<td>8</td>
<td>0.70(0.013) + 2.27(0.001) log(C:N)</td>
<td>32.45 0.30 79</td>
</tr>
</tbody>
</table>

*The p value of the parameters are presented between brackets.

*Inflow:evaporation ratio.

*The percentage of the lake’s volume filled with submerged vegetation (PVI) was augmented with 1% to avoid zero’s.

*The extinction of light at λ = 380 nm is used as a proxy for humic substances.

*Chlorophyll a concentration:extinction at λ = 380 nm ratio.

*Organic carbon: total nitrogen ratio in the top sediment.
Environmental Variables
For explanation of the variables, see Table 2.

Table 3. Multiple Linear Regression Models Describing the Relationship of Lakes’ Partial CO2 Pressure, Temperature, and Local Environmental Variables

<table>
<thead>
<tr>
<th>Coefficients</th>
<th>Intercept</th>
<th>Temperature</th>
<th>Inflow:evaporation</th>
<th>Chl a: humic</th>
<th>C:N</th>
<th>Regression Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F2 = 13.84</td>
<td>0.27</td>
<td>70</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>F3 = 12.59</td>
<td>0.35</td>
<td>67</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

4. Discussion

[18] The small fraction of lakes that is in equilibrium with the atmosphere indicates that most lakes were either sinks or sources to the atmosphere (Figure 2). As in surveys in other parts of the world [Cole et al., 1994; Sobek et al., 2003], most lakes were supersaturated, indicating that these lakes are net sources of CO2 to the atmosphere. In fact, pCO2 tends to be lowest in summer [Kelly et al., 2001] or dry season [Richey et al., 2002] precisely when our samples were taken. Therefore the annual average relative saturation per lake is likely even higher than we report here.

[19] The ratio between phytoplankton biomass and the light extinction at λ = 380 nm explained 21% (R 2) of the variation in pCO2 (Table 2). Most likely this is because the light extinction at this wavelength, which we used as a proxy for the level of humic substances can be used as an indicator for terrestrial carbon input. When the terrestrial carbon is mineralized this may lead to a net CO2 production. Phytoplankton, on the other hand, takes up CO2 during photosynthesis, reducing CO2 concentrations in the water. The higher the density of phytoplankton compared to the level of humic substances, the lower the pCO2 tends to be. Besides phytoplankton, submerged vegetation may contribute substantially to the primary production in shallow lakes thereby lowering the pCO2. Indeed, the pCO2 is systematically lower in lakes with high abundances of submerged vegetation (Table 2 and Figure 3).

[20] In other lake data sets, pCO2 was found to be positively correlated to DOC concentrations [Prairie et al., 2002; Sobek et al., 2003, 2005]. Although our lakes had a wide range in extinction at λ = 380 nm (used as a proxy for humic substances) and dissolved organic carbon (0.3–54.2 m−1 and 1.7–86 mg C L−1, respectively), we did not find a significant relation between pCO2 and the light extinction, and the explained variance in pCO2 by DOC was low (R2 = 0.08, Table 2). Our lakes, however, also covered a wide range in productivity and as pCO2 is influenced by primary production and respiration simultaneously, the chlorophyll a: of pCO2 (Table 3). At similar inflow:evaporation ratios, the cooler lakes had a lower pCO2 than the warmer lakes (Table 3, Figure 4a). In the same way, the warm lakes generally had a higher pCO2 than the cooler lakes at similar chl a: humic ratios (Table 3, Figure 4b).
humin substances ratio may therefore be most informative. A relatively constant primary production in comparison to the variation in DOC in the other data sets may explain the overruling influence of DOC on the pCO2 in those earlier studies. The strong correlation between DOC and chlorophyll a in our data set (R² = 0.48, p < 0.001) might indicate that in eutrophic lakes, much of the DOC is algal derived which may explain the negative correlation between pCO2 and DOC (Table 2).

[23] Our data furthermore suggest that hydrological characteristics of the lake, i.e., the ratio between inflow and evaporation, strongly affects the pCO2 (Table 2). In part this may reflect a temperature effect. Evaporation plays an important role in the energy budget of the lake and strong evaporation cools down the lake [Lenters et al., 2005]. Hydrology, however, also affects the input of terrestrial carbon to the lake. Indeed, pCO2 was generally high in lakes where the volume of incoming water from the watershed was large in comparison to the volume that had evaporated. The importance of lakes’ hydrology is in line with results from studies in other parts of the world [Algesten et al., 2004]. Although the pCO2 may be influenced by the inflow of CO2 rich groundwater as well [Striegl and Michmerhuizen, 1998], a dominant role of the terrestrial input in our lakes is suggested by the fact that 21% of the variance in pCO2 could be explained by the chlorophyll a: humic substances ratio.

[24] As an alternative indicator of the relative importance of terrestrial input, we analyzed the ratio between organic carbon and nitrogen in the sediment, a high C:N ratio indicating a relatively strong terrestrial influence on the lake’s metabolism. Indeed we found this indicator to explain a comparable part (30%) of the variance in pCO2 levels as the inflow:evaporation ratio (Table 2). Adding the ratios chlorophyll a: humic substances or C:N to regression models explaining pCO2 levels from the hydrology indicator did not add to the explanatory power (Table 3), suggesting that the hydrology might affect the carbon balance largely through its relative effects on allochthonous carbon input and in-lake primary productivity.

[25] For the lakes in our data set cooler lakes generally had a lower pCO2 than warmer lakes (Table 3); the coldest lakes in our data set generally being carbon sinks and the warmer lakes in our data set being carbon sources (Figure 3). To filter out the effects of idiosyncratic differences in terrestrial inputs and productivity among lakes we looked at relationships between pCO2 and the main indicators of these processes along the temperature gradient (Table 3, Figure 4). This again suggested a significant influence of temperature on the pCO2. At similar inflow:evaporation ratios, or similar chlorophyll a: humic ratios the warmer lakes had a higher pCO2 than the cooler lakes (Table 3, Figure 4). The logarithm of the pCO2 in lakes with a water temperature of 30°C was 0.3 to 0.4 units higher than in lakes with a water temperature of 20°C (see temperature regression coefficients Table 3), suggesting an approximate 2–2.5 times increase in pCO2 per 10°C in comparable lakes.

[26] Although the pCO2 is not a direct measure of the carbon flux in lakes, it is the most important factor influencing this flux [Sobek et al., 2005]. Therefore, our findings indicate a substantial influence of climate on CO2 efflux from lakes. The apparent effect of hydrology on the pCO2 in lakes suggested by our results implies that future changes in evaporation [Roderick and Farquhar, 2002] and precipitation regimes [IPCC, 2007] may have a strong impact on lake carbon emissions. In addition there is a clear relationship between pCO2 and temperature. Although clearly correlations do not give insight in causal relationships, various mechanisms could contribute to such a temperature effect. In addition to the direct effect of temperature on the CO2 flux (gasses dissolve better in colder than in warmer water), there is possibly an increase in net heterotrophy with temperature. Rates of respiration tend to increase stronger than production with temperature [Biddanda and Cotner, 2002; Lopez-Urrutia et al., 2006; Rivkin and Legendre, 2001; Sand-Jensen et al., 2007]. Importantly, the relatively strong
increase of respiration with temperature [Acuña et al., 2008] implies that warm lakes might metabolize a substantially larger portion of the terrestrial organic matter influx than cooler ones [Biddanda and Cotner, 2002; Jansson et al., 2008]. Primary production, on the other hand, may be limited by other factors than temperature (e.g., nutrients or light) this may prevent primary production from ‘keeping up’ with respiration when temperature increases.

5. Final Remarks

[25] Most likely, rising global temperatures will promote increased atmospheric greenhouse gas concentrations [Cox and Jones, 2008]. In fact, estimates based on ancient climate variation suggest that this effect may be quite large [Scheffer et al., 2006]. Future climate prognosis often neglect the feedback effect of temperature on greenhouse gas fluxes as our knowledge of the processes involved is insufficient leading to large uncertainties [Jones et al., 2006]. Our results suggest that warm inland waters emit more CO₂ than comparable cooler lakes. Carbon emission from cool lakes may therefore increase with climate warming. While this positive feedback mechanism has negative consequences from a climate change perspective, the sensitivity of the carbon balance of lakes to in-lake productivity and hydrology also suggests that a better understanding of the regulating mechanisms might give opportunities for managers to design climate friendlier management strategies of these hot spots of carbon channeling.

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References


