

Linking forest fires to lake metabolism and carbon dioxide emissions in the boreal region of Northern Québec

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Abstract

Natural fires annually decimate up to 1% of the forested area in the boreal region of Québec, and represent a major structuring force in the region, creating a mosaic of watersheds characterized by large variations in vegetation structure and composition. Here, we investigate the possible connections between this fire-induced watershed heterogeneity and lake metabolism and CO₂ dynamics. Plankton respiration, and water–air CO₂ fluxes were measured in the epilimnia of 50 lakes, selected to lie within distinct watershed types in terms of postfire terrestrial succession in the boreal region of Northern Québec. Plankton respiration varied widely among lakes (from 21 to 211 µg CL⁻¹ day⁻¹), was negatively related to lake area, and positively related to dissolved organic carbon (DOC). All lakes were supersaturated in CO₂ and the resulting carbon (C) flux to the atmosphere (150 to over 3000 mg C m² day⁻¹) was negatively related to lake area and positively to DOC concentration. CO₂ fluxes were positively related to integrated water column respiration, suggesting a biological component in this flux. Both respiration and CO₂ fluxes were strongly negatively related to years after the last fire in the basin, such that lakes in recently burnt basins had significantly higher C emissions, even after the influence of lake size was removed. No significant differences were found in nutrients, chlorophyll, and DOC between lakes in different basin types, suggesting that the fire-induced watershed features influence other, more subtle aspects, such as the quality of the organic C reaching lakes. The fire-induced enhancement of lake organic C mineralization and C emissions represents a long-term impact that increases the overall C loss from the landscape as the result of fire, but which has never been included in current regional C budgets and future projections. The need to account for this additional fire-induced C loss becomes critical in the face of predictions of increasing incidence of fire in the circumboreal landscape.

Keywords: boreal, carbon dioxide flux, climate, forest fire, lakes, organic carbon, plankton respiration, watershed

Received 5 November 2008; revised version received 8 April 2009 and accepted 15 April 2009

Introduction

There is increasing evidence that lakes and rivers play a significant role in regional carbon (C) budgets (Algesten *et al.*, 2003; Cole *et al.*, 2007). Lakes play a dual role in the regional C dynamics: On the one hand, they store significant amounts of C in their sediments (Einsele *et al.* 2001; Kortelainen *et al.*, 2006), and on the other,

they channel and release large amounts of C, both organic and inorganic, that originates in the terrestrial ecosystem (Kling *et al.* 1991). The most obvious evidence of this latter role is the consistent carbon dioxide (CO₂) supersaturation that characterizes most temperate and boreal lakes, which has been linked to several key processes at the whole ecosystem scale, such as ground water injection, carbonate dissolution, and photo-oxidation of dissolved organic C (DOC) (Hope *et al.*, 1996; Dillon & Molot, 1997; Sobek *et al.*, 2003). Several studies have further suggested that microbial

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degradation of allochthonous organic C, mostly as DOC, may also contribute significantly to CO₂ supersaturation and thus to CO₂ emission, especially in oligotrophic lakes (del Giorgio *et al.*, 1999; Jonsson *et al.*, 2003).

Regardless of the processes involved, CO₂ emission from lakes represents a net loss of C from the surrounding terrestrial ecosystems, but whether lakes act as vents of CO₂ that originates in the soils, or as reactors, converting terrestrial organic matter into CO₂ (and other gases such as CH₄), is central to our understanding of their role in the landscape. Given the key role that external organic matter plays in shaping lake metabolism and green-house gas dynamics, it is important to understand the features in the landscape that influence the delivery the organic matter into lakes. The geology, topography, and especially the nature of soils and of the plant cover of the terrestrial landscape all influence the export of materials, most notably organic matter, from land to lakes (Dillon & Molot, 1997; Huttunen *et al.*, 2003; Mattsson *et al.*, 2005).

Fire stands out as one of the key factors shaping the physiognomy of terrestrial landscapes in the boreal regions of Canada (Johnstone & Chapin, 2006). Wild fires annually decimate up to 1% of the total forested area in the boreal regions of North America (Chapin *et al.*, 2000; Bergeron *et al.*, 2001), and are a major structuring factor in the region, creating a mosaic of watersheds characterized by large variations in vegetation structure and composition (Arsenault, 2001). The changes in land cover following forest fires, and the resulting shifts in C and nutrient export and water movement could impact the functioning of the receiving lakes. Several studies have shown significant biogeochemical and biological impacts after fire, such as increases in biomass and changes in community structure of phytoplankton (Planas *et al.*, 2000) and zooplankton (Patoine *et al.*, 2000). However, the effect of fire on lake C metabolism has not been well explored. Respiration is fueled primarily through the consumption of dissolved organic matter, which offers both a connection to surrounding watersheds (Lennon & Pfaff, 2005), and to natural CO₂ dynamics in lakes. The movement of materials immediately following a natural fire is usually intense (Certini, 2005), and the secondary plant succession results in a recovery of both soils and plant cover, immobilization of nutrients, and changes in the pathways of C and water (Certini, 2005), with a general decrease in runoff and material export from the watershed.

Understanding of the links between lake C dynamics and landscape features is particularly important in the northern Canadian boreal landscape, where lakes occupy between 10% and 15% of the total surface (Downing *et al.*, 2006; Teodoru *et al.*, 2009). Most of these high-

latitude freshwater ecosystems are oligotrophic, and there are indications that most act as net sources of CO₂ to the atmosphere (Planas *et al.*, 2005; Roehm *et al.*, 2009), as has been reported for boreal lakes elsewhere (Sobek *et al.*, 2003). Fire imposes a large degree of landscape heterogeneity at relatively small spatial scales in this region, and in this paper we explore the links between basin characteristics, lake metabolism and lake greenhouse gas dynamics. In particular, we address the question: Does landscape heterogeneity resulting from forest fires influence C metabolism and CO₂ dynamics in boreal lakes? To address this question, we conducted a comparative study of plankton respiration and air–water CO₂ fluxes in 50 lakes that varied in lake and watershed size, located in watersheds at different postfire successional stages in the Eastmain region of boreal Québec.

Materials and methods

Site description and experimental approach

Three sampling campaigns were conducted during the summer and autumn of 2006 in the Eastmain region (51–52°N, 75–76°W), of northern Québec, Canada. The Québec boreal forest covers over 900 000 km², representing near 70% of the total territory. Evergreen species are dominant in mature forests and mostly consist of black spruce (*Picea mariana*), and to a lesser extent, white spruce (*Picea glauca*), American larch (*Larix laricina*), Jack pine (*Pinus banksiana*) and the balsam fir (*Abies balsamea*). Deciduous trees, which dominate early forest successional stages, include the quaking aspen (*Populus tremuloides*), the black cottonwood (*Populus trichocarpa*) and the paper birch (*Betula papyrifera*). The region is characterized by an average temperature varying between 0 and –2.5 °C, with 600–1000 mm of annual precipitations, and with an average altitude of 250 m. Freshwaters (lakes, rivers and wetlands) cover over 20% of the territory, with extensive bogs and peatlands in addition to complex networks of rivers and lakes (Teodoru *et al.*, 2009).

A total of 50 lakes were sampled for this study: forty-two lakes were sampled once in one of the three field campaigns (June, August and September) during the summer and autumn of 2006, and eight reference lakes were sampled three times (once for every campaign), to assess potential seasonal variability in the parameters measured. Owing to the remoteness of the study site, sampling was carried out using helicopters or hydroplanes. The lakes were selected to lie within homogenous drainage basins in terms of the physiognomy of terrestrial vegetation, which in turn is driven mostly by the time since the last fire event.

There are few headwater lakes in the dataset. The initial selection was carried out with a combination of satellite images, used to characterize the target basins types and lakes, and Geographic Information System (GIS) to determine lake position and morphometry. We used satellite pictures from Google Earth 3.1 (2006), to select homogenous successional patches composed of either recently burned, young regeneration or mature stands. We then used data from the Société de Protection des Forêts contre le Feu (SOPFEU), the Québec provincial agency responsible for fire management, to confirm the exact year of burning. Lakes were selected from seven different regions associated with a respective year of fire. Each region is associated to a unique fire event to reduce bias related to fire properties (type, intensity). Overall, we generated five categories of basins in terms of fire history: <1983 (mature stands), 1989, 1995–1997, 2002, 2006 for analysis. Lake and watershed morphometry was determined using ARCMAP 9.1 GIS and XTOOLS PRO extension for calculations.

Sampling and in situ measurements

Dissolved oxygen, water temperature, pH, conductivity, and lake depth were measured *in situ* with an YSI probe. Because there is no bathymetry available for any of these remote lakes, we measured depth at multiple sites within a lake to determine the deepest point, which was selected for sampling and gas flux measurements. CO₂ fluxes at the water–air interface were measured *in situ* using an air- and light-proof floating chamber (24 cm × 37 cm × 14 cm) connected to an infrared gas monitor (EGM-4, PP systems, Amesbury, MA, USA). Readings of CO₂ concentration in the chamber headspace were taken each minute for 10 min, and replicate chamber experiments were carried in each lake; due to logistical constraints, flux measurements were carried out in 42 out of all 50 lakes sampled. A complete temperature and oxygen profile was carried out with a YSI meter, and a water sample was collected at 1 m below the surface using a peristaltic pump into acid-clean 4 L cubitainers, which were placed in the dark in a cooler. Up to three lakes were visited each day, so the water samples were stored from 2 to 6 h in the coolers before being processed back in the laboratory.

Respiration measurements

Plankton respiration was determined from changes in oxygen concentrations during *in vitro* incubations in the dark. Replicate 500 mL erlenmeyers, were filled for each lake sample, sealed with silicone stoppers, and placed

in cooler immersed in circulating water that was kept at ambient epilimnetic temperature by a circulating water bath. O₂ concentrations were measured using an optrode system, consisting of oxygen-sensitive optical sensors and a fiber optic meter (Fibox 3, PreSens, Regensburg, Germany), following Kragh *et al.* (2008), who were among the first to use this approach to measure respiration in natural water samples. The principle of the sensor operation is based on the quenching of fluorescence of a dye caused by contact with molecular oxygen. A circular, 5 mm optical sensor was glued to the inside bottom part of each erlenmeyer with a silicone glue provided by the manufacturer. Dissolved oxygen measures were taken through the glass wall by illuminating the sensor with the optic fiber and recording the fluorescence emission of the sensor. Because the distance and angle between the sensor and fiber optic probe, as well as ambient light, may influence the readings, we constructed an enclosed system composed of a box and a base holding the sensor, which allowed the erlenmeyers to be placed always at the same distance and position relative to the optical fiber, and minimized interference by ambient light.

The quenching of the fluorescence emission from the sensor by O₂ is very sensitive to temperature fluctuations, and thus a stringent temperature control is required to achieve the necessary level of precision. The Fibox 3 system is equipped with a temperature probe that is independent from the optical probe, and which is meant to be placed as close to the O₂ sensor as possible to capture the local variations in temperature and correct the readings consequently. Our experimental set up, composed of sealed erlenmeyers, did not allow to place the temperature probe directly next to the O₂ sensor, and thus to adequately control for temperature. For this reason, a third erlenmeyer per lake was used as a control to follow any temperature variations in the incubation system. This control erlenmeyer was not sealed so that the temperature probe could be placed at the bottom in the same location of the O₂ sensors in the sealed erlenmeyers, and was handled in exactly the same way as the latter, so as to capture any possible temperature fluctuations during measurement.

The samples were allowed to equilibrate for at least 30 min immersed in the water bath before the initial oxygen reading was taken. Repeated measures (10 successive oxygen readings on the same sensor during the course of 2 min after a 30 s stabilization) were taken from each flask at 12 h intervals for 60 h. The protocol that we used allowed us to attain an average standard error of $\pm 30 \mu\text{g O}_2 \text{ L}^{-1}$ for repeated measures on the same sensor, which is lower than the $50 \mu\text{g O}_2 \text{ L}^{-1}$ reported by the manufacturer.

Laboratory analyses

Rates of bacterial production (BP) were estimated from the uptake of ^3H -leucine following the centrifugation method of Smith & Azam (1992). The final tritiated leucine concentration in all experiments was 40–60 nM, based on preliminary experiments that showed that uptake rates were maximal in this range. DOC concentrations in 0.2 mm filtered sample water were measured in an OI-1010 Total Carbon Analyzer (OI Analytical, TX, USA) using wet persulphate oxidation. Total phosphorus (TP) was determined by the molybdenum-blue method after persulphate digestion, and total nitrogen (TN) was measured as nitrates after alkaline persulphate digestion. Chlorophyll *a* (Chl*a*) was measured spectrophotometrically in ethanol extracts.

Statistical analyses

For comparisons among lakes, all data were log-transformed to meet normality assumptions and to equalize variances. Pair-wise correlations were performed between environmental variables and respiration to determine the major significant correlations ($P < 0.05$). One-way ANOVA was used to explore the distribution of lake surface among basin types, and to assess potential intercampaign variations in terms of respiration rates and other environmental variables in the reference lakes. ANOVA was also used to assess the influence of basin type on TP, TN, DOC, and Chl*a*. Least squares linear regression was used to assess relations between lake area, lake area to watershed area ratio and respiration and CO_2 flux rates. Multiple regression analysis was used to assess combined effects of lake morphology and basin type on respiration and CO_2 fluxes. All data analyses were conducted using JUMP 5.0.1a statistical software (SAS Institute Inc., Cary, NC, USA).

Results

General characteristics of lakes and basins

A total of 50 lakes were sampled in this study, on the basis of having basins characterized by homogenous vegetation stands of different ages, related to the fire history. When assessed *in situ*, 34 of the selected basins had homogenous vegetation structure that agreed well with the *a priori* GIS- and satellite-based characterization; 16 other watersheds had mixed vegetation resulting of multiple fire events or other topographical features that were not well detected using remote sensing. Owing to this heterogeneity in terrestrial vegetation, we excluded the data from the lakes in these basins

from the analysis of effect of basin type; we used the complete lake dataset for all other analyses.

Lake area (L_A) ranged from 0.007 to 56.1 km² [mean 2.2 ± 8.5 (SD) km²] and maximum recorded depths varied from 1 to 23.6 m (mean 6.2 ± 5.2 m), and were positively correlated to each other ($r^2 = 0.38$, $n = 50$, $P < 0.0001$). Total watershed area (W_A) ranged from 0.147 to 142.3 km² (mean 9.2 ± 22.2 km²) and was also positively related to L_A ($r^2 = 0.57$, $n = 50$, $P < 0.0001$), yet the ratio lake to watershed area (L_A/W_A) still varied widely, from 0.001 to 0.52. No significant differences were observed in the eight reference lakes between the three sampling periods (June, August, and September) in terms of nutrients (ANOVA: TP, $P = 0.08$; TN, $P = 0.58$), Chl*a* (ANOVA: $P = 0.37$), DOC (ANOVA: $P = 0.77$), respiration ($P = 0.44$), or CO_2 fluxes ($P = 0.18$). We therefore used the mean of the three samplings of the eight reference lakes for all selected parameters, and did not correct the data for the other lakes for possible temperature or other seasonal biases.

Patterns in nutrients and lake characteristics with drainage basin type

Despite the large range in L_A , depth, and W_A , there was a relatively narrow range in several key lake characteristics (Table 1). For example, TP varied from 5.1 to 32.4 $\mu\text{g L}^{-1}$ (mean 12.1 ± 4.8 $\mu\text{g L}^{-1}$), TN varied from 154 to 483 $\mu\text{g L}^{-1}$ (mean 280 ± 70 $\mu\text{g L}^{-1}$), and Chl*a* from 1.7 to 5.6 $\mu\text{g L}^{-1}$ (mean 3.1 ± 0.9 $\mu\text{g L}^{-1}$) (Table 1). TP and TN were positively correlated ($r^2 = 0.42$, $n = 50$, $P < 0.0001$), but neither of the two nutrients was significantly correlated to Chl*a*. DOC varied from 4.2 to 17.5 mg L^{-1} (mean 8.8 ± 3.1 mg L^{-1}), and was weakly related with TP ($r^2 = 0.23$, $n = 50$, $P = 0.0004$) and TN ($r^2 = 0.40$, $n = 50$, $P < 0.0001$). DOC was also negatively related with L_A ($r^2 = 0.19$, $n = 50$, $P = 0.0013$) and depth ($r^2 = 0.34$, $n = 50$, $P < 0.0001$), but had no relationship with W_A or chlorophyll concentrations.

There were no significant relationships between the basin type and TP (ANOVA, $n = 34$, $P = 0.54$), TN (ANOVA, $n = 34$, $P = 0.85$), Chl*a* (ANOVA, $n = 34$, $P = 0.11$) and DOC (ANOVA, $n = 34$, $P = 0.35$). There were no significant relationships between these same parameters even after the influence of L_A was accounted for using multiple regression. Furthermore, a multiple regression including L_A shows no significant changes in the ratio of absorbance (ABS_{440}) to DOC ($\text{ABS}_{440}/\text{DOC}$) across basin types.

Patterns in plankton respiration and BP

Nine individual respiration time courses out of 140 that were carried out were rejected because of erratic oxygen

Table 1 Data table for all lakes sampled between the months of May and October 2006

Lake	L_A (km ²)	Z (m)	W_A (km ²)	TP	TN	DOC	Chl <i>a</i>	BP	R	CO ₂ flux	Year of fire
Natel	3.867	11.8	17.113	7.42	0.196	5.91	2.19	2.16	33.90	227	<1983
Lac 11	0.376	2.3	2.506	12.8	0.286	8.34	3.35	6.16	54.23	157	<1983
Lac 8	0.317	8.7	2.801	11.35	0.177	5.93	3.15	4.52	57.15	247	<1983
Labyrinthe	2.574	12.2	10.476	10.32	0.242	8.15	3.67	3.85	43.20	294	M
Clarkie	24.694	13.0	61.900	8.41	0.165	5.32	2.37	2.53	36.00	211	M
Brendan	1.068	14.0	3.555	6.87	0.235	5.43	4.20	3.18	64.05	203	1995
EM-320	0.476	5.2	4.542	12.66	0.264	7.17	3.01	5.16	53.10	372	M
Mistumis	3.970	7.7	19.082	12.2	0.237	6.91	3.82	6.35	37.58	511	M
L-4	0.010	2.0	1.366	11.03	0.269	8.79	2.05	5.70	108.90	794	na
L-5	0.011	0.7	10.212	15.18	0.376	9.20	3.36	15.42	210.60	587	na
L-7	0.189	0.7	1.966	17.97	0.483	9.40	1.98	18.13	60.75	225	na
L-9	0.105	4.7	0.961	16.46	0.401	8.67	2.05	6.29	40.50	na	<1983
L-11	0.010	4.5	0.147	14.11	0.256	14.54	2.02	10.07	75.60	3281	na
L-12	0.228	6.2	5.452	8.89	0.349	6.67	2.58	3.45	57.15	na	na
L-14	0.074	4.8	2.695	9.46	0.257	7.61	3.45	5.56	117.90	1604	1995
L-15	0.015	0.8	5.409	10.03	0.268	15.25	2.02	13.26	132.30	na	1995
L-16	0.012	1.6	0.162	11.89	0.298	8.29	2.58	7.38	69.30	na	<1983
L-17	0.037	1.9	0.161	19.18	0.280	5.25	4.78	11.84	100.80	430	na
L-18	0.042	5.9	3.190	18.04	0.252	6.15	3.54	5.40	33.30	na	<1983
L-19	0.032	2.0	5.973	32.40	0.368	15.06	5.59	6.69	90.00	594	na
L-20	0.601	23.6	2.063	6.17	0.213	5.00	3.47	2.50	72.90	na	2002
L-21	0.007	1.0	2.393	12.82	0.259	9.86	2.44	9.64	101.25	na	2002
L-24	0.084	3.6	2.344	16.04	0.345	9.28	2.19	9.08	81.00	1167	2006
L-25	0.058	3.1	0.971	10.75	0.216	9.16	3.04	9.90	72.45	na	2006
L-26	0.156	5.4	0.739	11.32	0.230	8.67	4.11	6.03	93.60	618	2006
L-27	0.016	2.5	0.396	15.03	0.333	14.30	2.48	9.33	77.40	1428	2006
L-28	0.405	5.5	1.465	10.60	0.268	7.92	2.76	4.67	66.15	505	2006
L-34	0.459	8.8	4.329	8.50	0.280	7.77	4.21	5.87	34.20	448	<1983
L-38	0.251	10.8	2.655	8.57	0.227	7.77	4.11	7.06	35.10	332	na
L-39	0.821	3.2	6.514	10.76	0.267	7.78	3.54	2.88	34.75	206	1995
L-40	0.162	9.8	1.855	10.23	0.208	5.22	3.79	6.88	34.75	744	1995
L-41	1.095	1.1	11.485	11.16	0.362	7.98	4.45	2.85	36.45	621	1995
L-42	0.346	2.3	1.927	11.22	0.343	9.75	3.75	2.51	41.85	343	1989
L-43	0.485	8.3	0.930	11.00	0.304	9.43	4.00	6.24	45.90	327	1989
L-44	4.298	7.4	46.285	20.28	0.282	10.54	4.60	1.81	43.65	749	1989
L-45	56.124	12.0	142.316	21.34	0.323	11.46	2.55	2.72	45.00	877	1989
L-46	1.956	21.8	7.297	6.96	0.192	5.37	3.56	2.63	35.55	512	1989
L-47	0.476	6.3	3.368	9.09	0.279	9.16	4.21	2.34	45.00	739	1989
L-48	1.049	5.3	5.042	10.40	0.242	6.55	3.43	2.79	21.15	655	<1983
L-49	1.234	1.5	6.049	10.73	0.312	9.34	3.29	6.02	64.35	341	<1983
L-50	0.885	14.7	3.667	5.67	0.176	6.31	2.90	1.38	28.35	290	<1983
L-54	0.028	1.3	0.674	9.76	0.316	11.66	1.70	6.05	32.40	355	<1983
L-56	0.065	7.1	0.512	7.50	0.172	4.23	2.97	3.21	54.90	273	<1983
L-59	0.030	4.6	0.592	8.39	0.284	12.22	2.02	2.37	63.00	310	na
L-60	1.380	13.1	9.340	5.09	0.154	5.49	3.37	0.67	49.95	239	na
L-62	0.024	2.5	0.661	16.36	0.411	17.55	2.76	5.64	86.40	919	1997
L-63	0.018	1.25	0.352	10.38	0.307	15.07	2.97	4.86	72.45	383	1997
L-66	0.072	6.0	0.923	12.23	0.323	7.89	2.12	2.39	44.55	1411	M
L-67	1.458	3.5	18.363	18.28	0.355	7.30	2.33	2.85	53.55	539	M
L-70	0.053	0.6	9.455	10.45	0.388	11.99	1.91	3.21	96.30	1782	2002

L_A , lake area; Z, depth; W_A , watershed area; TP, total phosphorus ($\mu\text{g L}^{-1}$); TN, total nitrogen (mg L^{-1}); DOC, dissolved organic carbon (mg L^{-1}); Chl*a*, chlorophyll *a* ($\mu\text{g L}^{-1}$); BP, bacterial production, $\mu\text{g C L}^{-1} \text{day}^{-1}$; R, plankton respiration ($\mu\text{g C L}^{-1} \text{day}^{-1}$); CO₂ flux ($\text{mg C m}^{-2} \text{day}^{-1}$); M stands for mixed basins in terms of fire.

readings. Although all incubations lasted 60 h, for most of the samples the first 24 h yielded robust time courses; 13 out of 70 samples had noisier initial patterns and in these samples we used the measurements up to 60 h to calculate O₂ consumption. The O₂ decline over 60 h was in most cases linear so that use of 24 or 60 h did not yield significantly different results.

Plankton respiration rates ranged 10fold across lakes, from 21.2 to 210.6 µg C L⁻¹ day⁻¹ (mean 62.8 ± 33.2 µg C L⁻¹ day⁻¹) among the 50 lakes studied in the Eastmain region (Table 1). BP was even more variable across lakes, ranging over 25fold, from 0.7 to 18 µg C L⁻¹ day⁻¹ (mean 5.6 ± 0.51 µg C L⁻¹ day⁻¹). Respiration and BP were positively correlated [Fig. 1, Eqn (1), Table 2]. Pair-wise correlations showed no significant relationships between respiration and TP or Chl_a, and only a very weak correlation with TN. In contrast, respiration was positively correlated to DOC ($P = 0.0048$, $n = 50$).

Respiration was related to lake morphometry, both to depth ($P = 0.001$, $n = 50$, not shown), and to lake area [Fig. 2a, Eqn (2), Table 2], and also to the ratio of lake area to watershed area [L_A/W_A , Fig. 2b, Eqn (3), Table 2], whereas basin area alone was marginally significant ($P = 0.048$, $n = 50$). The best individual regression models had lake area and the ratio of lake to watershed [Eqns (2) and (3), Table 2]. These individual regression models suggest that smaller lakes, and lakes that have relatively large drainage basins, tend to have higher rates of water column respiration.

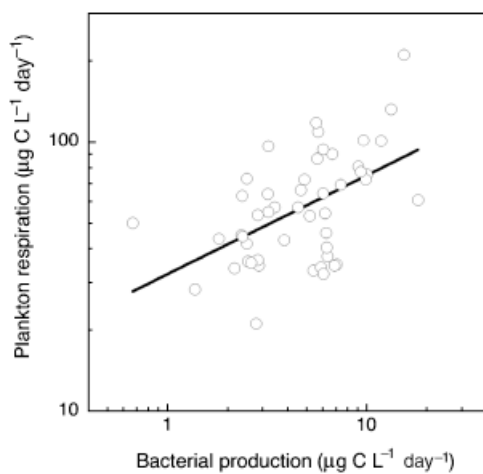


Fig. 1 The relationship between plankton respiration and bacterial production. Data are log-transformed, and regression equation is given in text.

Patterns in air–water CO₂ flux

We measured positive (water to atmosphere) CO₂ fluxes in all lakes sampled, and CO₂ fluxes varied from 90 to 3000 mg C m² day⁻¹ (mean 587 ± 575 mg C m² day⁻¹). Pair-wise correlation analysis showed significant positive relationships between CO₂ fluxes and DOC ($r^2 = 0.19$, $n = 42$, $P = 0.0035$), and negative correlation with secchi depth ($r^2 = 0.35$, $n = 34$, $P = 0.0002$) and pH ($r^2 = 0.38$, $n = 42$, $P < 0.0001$). As with planktonic respiration, CO₂ flux was negatively related to lake area and the lake/basin ratio [Fig. 3a and b; Eqns (4) and (5), Table 2].

Influence of fire history on respiration and CO₂ fluxes

The type of basin, expressed as years after fire (YAF), had a strong influence on both respiration and CO₂ fluxes [Eqns (6) and (7), respectively, Table 2]. For any given lake or watershed size, respiration rates tended to be higher in lakes located in watersheds that were recently burned compared with those within mature forested areas (Fig. 2c and d). In fact, the best multivariate regression model of water column respiration,

Table 2 Single and multiple regression models between the key variables

Model	<i>N</i>	<i>r</i> ²	<i>P</i>	Eqn
Log- <i>R</i> = 1.58 [0.04] + 0.33 [0.06] Log-BP	50	0.31	<0.0001	(1)
Log- <i>R</i> = 2.46 [0.13] - 0.13 [0.02] Log- <i>L</i> _A	50	0.37	<0.0001	(2)
Log- <i>R</i> = 1.52 [0.04] - 0.21 [0.03] Log- <i>L</i> _A / <i>W</i> _A	50	0.38	<0.0001	(3)
Log-CO ₂ = 3.39 [0.25] - 0.13 [0.05] Log- <i>L</i> _A	46	0.27	<0.0001	(4)
Log-CO ₂ = 2.44 [0.09] - 0.24 [0.08] Log- <i>L</i> _A / <i>W</i> _A	46	0.29	<0.0001	(5)
Log- <i>R</i> = 1.93 [0.05] - 0.01 [0.003] YAF	34	0.39	<0.0001	(6)
Log-CO ₂ flux = 2.99 [0.09] - 0.02 [0.006] YAF	29	0.36	0.001	(7)
Log- <i>R</i> = 2.36 [0.15] - 0.01 [0.002] YAF - 0.09 [0.03] Log- <i>L</i> _A	34	0.52	<0.0001	(8)
Log-CO ₂ flux = 1.75 [0.45] - 0.02 [0.005] YAF - 0.32 [0.09] Log- <i>L</i> _A + 0.45 [0.12] Log- <i>W</i> _A	30	0.60	<0.0001	(9)
Log-CO ₂ flux = 2.31 [0.26] + 0.41 [0.13] Log- <i>R</i> _A - 0.65 [0.12] Log-Chl _a _A	47	0.41	<0.0001	(10)

Values in parentheses are standard error of the estimates. YAF, year after fire; *R*_A, integrated *R* over mixed layer (mg C m⁻² day⁻¹), and Chl_a_A, integrated chlorophyll over photic zone (mg m⁻²; all other variables as in Table 1).

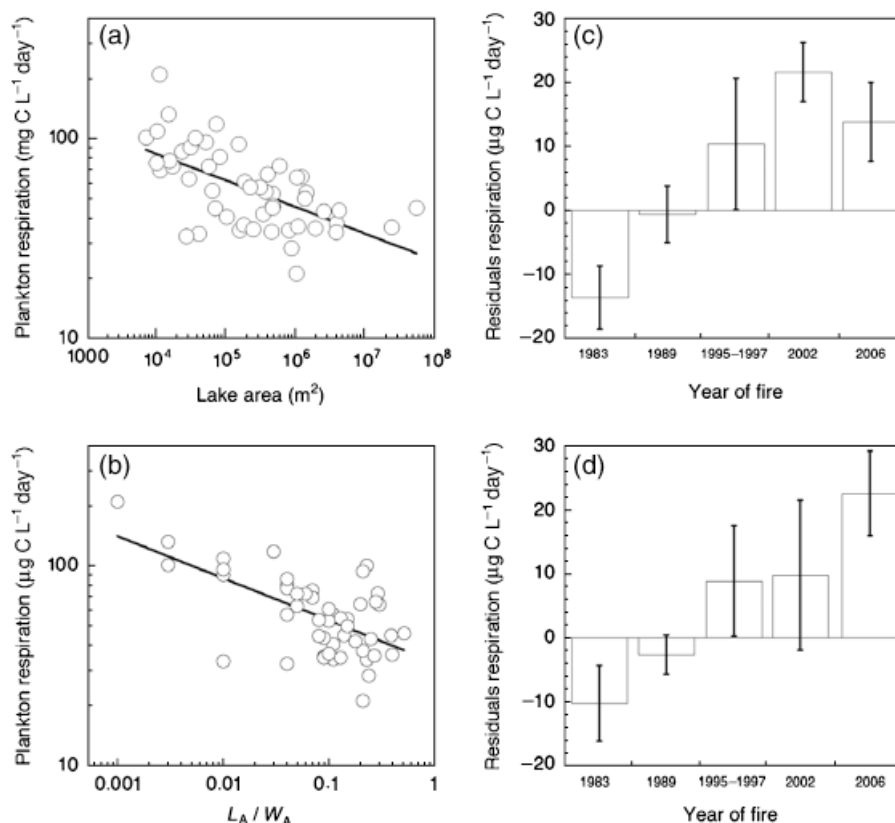


Fig. 2 Plankton respiration as a function of (a) lake area and (b) lake area/watershed area ratio (L_A/W_A). Data are log-transformed and the full regression equations are given in text. (c) and (d) are the residuals of the respiration-area (c) and respiration- L_A/W_A (d) relationships as a function of years since the last fire in the basin.

based on the subset of 34 lakes that lie within well-characterized basins in terms of fire impact, included both L_A ($P < 0.006$) and basin type, expressed as YAF ($P < 0.0004$) as independent variables [Eqn (8), Table 2].

Likewise, fluxes were significantly higher in lakes surrounded by watersheds that were recently burned compared with those within mature forested areas, once the effect of L_A and W_A was removed (Fig. 3c and d). Multiple least square regression shows, in addition to the type of basin effect, a negative correlation between fluxes and L_A and a positive correlation with W_A [Eqn (9), Table 2]. This regression model suggests that CO₂ fluxes tend to be higher in smaller lakes, and that for a given lake size, fluxes tend to be lower in lakes with smaller basins relative to the lake surface, and also in lakes that have basins dominated by mature forest as opposed to having been recently burned.

Connections between CO₂ and water column metabolism

We further explored the possible connections between the measured CO₂ flux and both water column respiration and the trophic status of the lake (indicated by the chlorophyll concentration). Volumetric rates of respira-

tion were only marginally positively correlated to flux, explaining 13% of the variability (data not shown), whereas chlorophyll was not correlated to flux at all. These relationships become stronger when we used the respiration rates integrated over the depth of the epilimnion in stratified lakes, and over total depth in mixed lakes, and chlorophyll concentrations integrated over the photic depth [Eqn (10), Table 2]. The resulting model explains over 40% of the variability in CO₂ flux and shows that areal respiration is significantly positively, and areal chlorophyll negatively correlated to fluxes.

We further estimated the potential contribution of water column R to the measured CO₂ fluxes by integrating R over the mixed layer (or total lake depth in case of shallow or destratified lakes), and then subtracting the potential photosynthetic CO₂ uptake, which we calculated based on chlorophyll using from the empirical model in del Giorgio & Peters (1994) and integrated over the photic layer, the latter based on Secchi depth measurements. This calculation shows that pelagic respiration may account anywhere from <10% to essentially the entire CO₂ flux observed in these lakes, and that this contribution is a strong positive function of lake depth (Fig. 4).

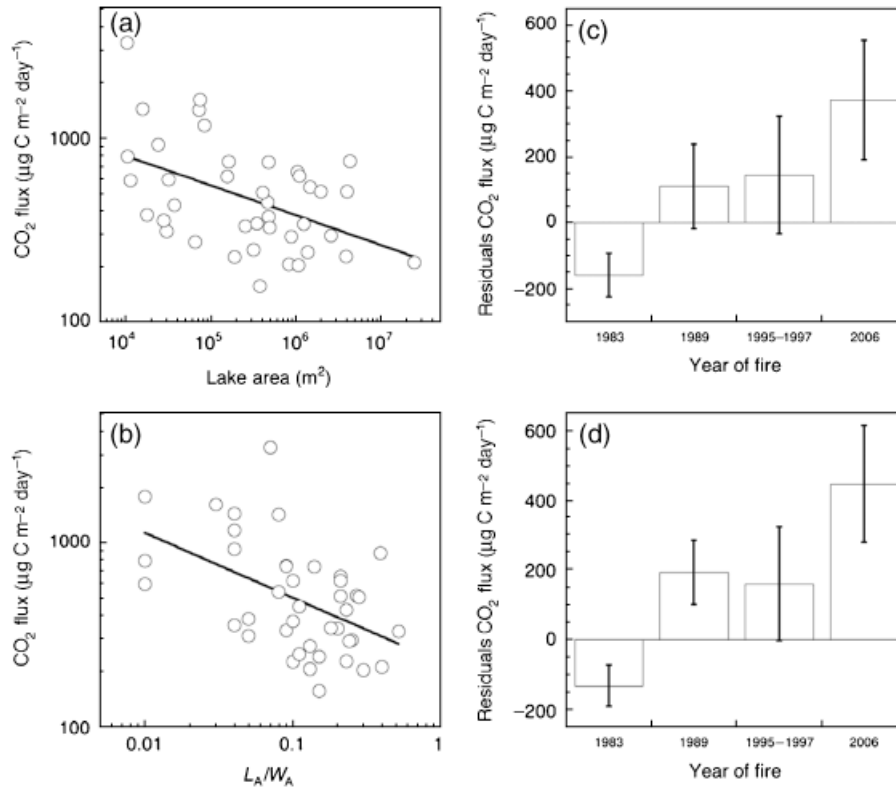


Fig. 3 CO₂ flux as a function of (a) lake area and (b) L_A/W_A. Data are log-transformed and the full regression equations are given in text. (c) and (d) are the residuals of the flux-area (c) and flux-L_A/W_A (d) relationships as a function of years since the last fire in the basin.

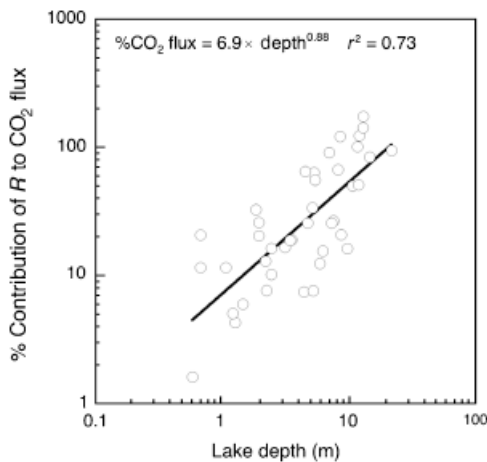


Fig. 4 The potential contribution of integrated water column respiration to the measured CO₂ flux, as a function of lake depth.

Discussion

Previous studies have unequivocally established that most boreal lakes are systematically supersaturated in CO₂ and emit significant amounts of C to the atmo-

sphere (Dillon & Molot, 1997; Kelly *et al.*, 2001; Algesten *et al.*, 2003; Sobek *et al.*, 2003; Roehm *et al.*, 2009). There is consensus that lake CO₂ supersaturation represents a loss of terrestrial C, but the origin of this C and the pathways that lead to the CO₂ emissions have yet to be understood. A handful of studies have attempted to link these lake C dynamics to climate (Sobek *et al.*, 2003) and watershed physiognomy (i.e. Huttunen *et al.*, 2003; Jansson *et al.*, 2008), and to DOC loading (Hope *et al.*, 1996; Prairie *et al.*, 2002; Jonsson *et al.*, 2003), yet the underlying mechanisms and the links between watershed features and CO₂ fluxes remain unclear. Our results confirm that the boreal lakes in Northern Québec all have significant fluxes of CO₂ to the atmosphere; we have further shown that these fluxes are linked to epilimnetic respiration, and that both CO₂ fluxes and epilimnetic respiration tended to be higher in smaller lakes, lakes with large watersheds, and also in lakes with higher DOC concentrations. More importantly, we have shown a clear link between both CO₂ fluxes and epilimnetic plankton respiration with watershed physiognomy in terms of postfire successional stage. We discuss the implications of these findings in the sections below.

Patterns in epilimnetic respiration

Epilimnetic water column respiration has been previously related to lake trophic status (TP and Chl_a), and to DOC content (del Giorgio *et al.*, 1999; Pace & Prairie, 2005), but in our dataset neither TP nor chlorophyll were significantly related to respiration. However, when placed in the larger context of previously published data from lakes worldwide, mostly from temperate regions (taken from Pace & Prairie, 2005), our respiration data fall roughly in the expected region relative to TP and chlorophyll (Fig. 5a and b), so the lack of relationship may be due to the relatively narrow range in lake trophy found in our lakes. Our data did show a weak but significant positive relationship between DOC and respiration, suggesting that in this boreal region, differences in external organic C loading are more important in driving ecosystem metabolism than differences in autochthonous primary production. This relationship had been reported before for lakes worldwide (Pace & Prairie, 2005), but interestingly, for any given concentration of DOC (in the range of 4–20 mg L⁻¹), respiration in our boreal lakes appears to be on average 50% lower than that reported for lakes in other, mostly temperate regions (Fig. 5c). There may be systematic latitudinal differences in the composition of terrestrial vegetation that result in differences in DOC loading and quality (Melillo *et al.*, 1984; Mattsson *et al.*, 2005), such that lake metabolism per unit DOC loading varies, yet other reports show no effect of DOM source on lake bacterial respiration and growth efficiency (Lennon & Pfaff, 2005). This is an issue that needs to be investigated further.

Lake size and the ratio of lake to basin area were strongly related to epilimnetic respiration in these boreal lakes. Previous studies have reported links between lake area and lake metabolism. For example, Sand-Jensen & Staehr (2007) also found a strong size scaling of lake metabolism in Danish lakes, despite a much narrower range in lake sizes (0.0002–0.22 km²) than the one reported here (0.007–56.12 km²). Likewise, the work of Biddanda *et al.* (2001) also suggests a size-scaling of pelagic metabolism in northern temperate lakes. The size-scaling of pelagic metabolism is most likely linked to higher material loading per unit lake area in smaller lakes, and the resulting lower nutrient and DOC concentrations due to longer residence times typically found in larger lakes.

Patterns in CO₂ fluxes

The air–water CO₂ fluxes that we report here are derived from floating chamber measurements, an approach that has been taken by others before (i.e. Huttu-

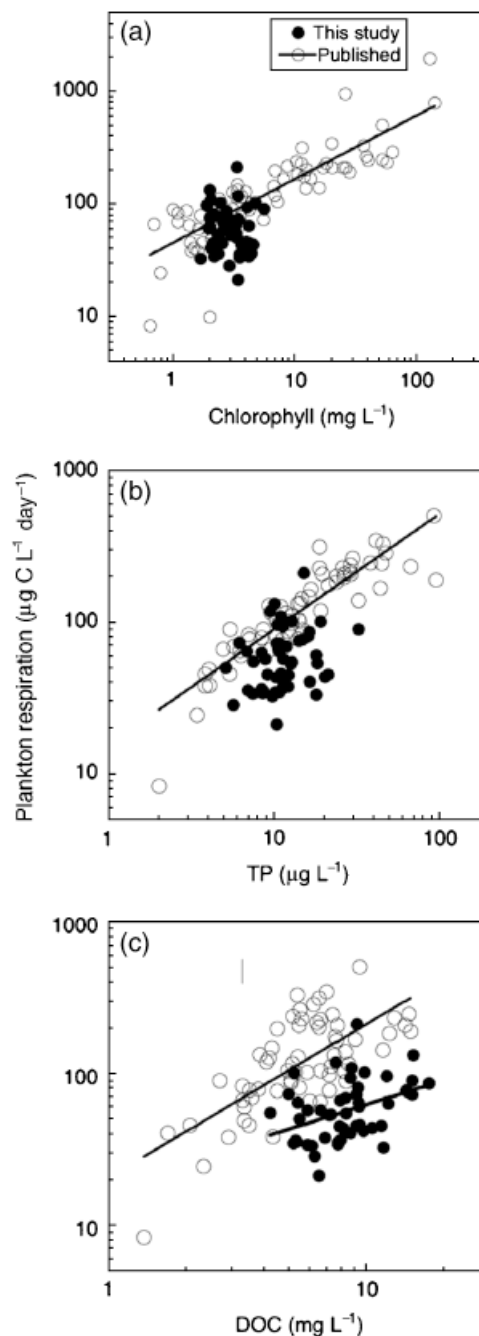


Fig. 5 Plankton respiration as a function of chlorophyll *a* (a), total phosphorus (TP) (b), and dissolved organic carbon (DOC) (c). Dark circles are the data for the boreal Québec lakes presented in this study, open circles are published data for lakes worldwide, compiled by Pace & Prairie (2005). Data are log-transformed, and the regression equation for DOC is presented in the text.

nen *et al.*, 2003). Most previous studies have estimated CO₂ fluxes from either surface water *p*CO₂ (del Giorgio *et al.*, 1999; Kelly *et al.* 2001; Algesten *et al.*, 2003; Jonsson

et al., 2003), or indirectly from C mass balances (Dillon & Molot, 1997; Algesten *et al.*, 2003; Sobek *et al.*, 2003), and there is evidence that these various approaches may yield quite different results. In particular, fluxes based on direct chamber measurements tend to be higher than those based on $p\text{CO}_2$ and assumptions on wind speed (Y. T. Prairie, personal communication, Matthews *et al.*, 2003). Clarifying these discrepancies is beyond the scope of this paper, but we argue that while the magnitude of the flux (and thus of some of the calculations that we present below) may have to be eventually adjusted, there are no known biases in the approaches we used that could generate the actual patterns relative to fire that we have observed.

There was a two-order of magnitude range in measured CO_2 fluxes across the lakes sampled, a range larger than any other limnological or biological variable that we measured. DOC explains a small but significant fraction of the variability in fluxes, as has been shown previously for other regions (Hope *et al.*, 1996; Prairie *et al.*, 2002; Jonsson *et al.*, 2003). We have also shown that 40% the variability in the lake CO_2 fluxes could be explained by a combination of integrated respiration and chlorophyll, further suggesting that at least a portion of this flux originates from biological activity within the lake, and that local primary production modulates this process, as has been reported in other studies (Prairie *et al.*, 2002; Huttunen *et al.*, 2003; Prairie, 2008). In this regard, we have shown that water column respiration may account for essentially all the flux in deep lakes, but only a small fraction of it in shallower lakes (Fig. 4), suggesting that sediment metabolism, which we did not include in our analysis, plays a major role in determining CO_2 dynamics in these (overwhelmingly shallow) lakes, as have been shown for other boreal regions (Sobek *et al.*, 2003; Kortelainen *et al.*, 2006).

Influence of fire on lake respiration and CO_2 flux

The major finding of this study is that the history of fire in the watershed, here expressed as years since the last recorded event (YAF), has a highly significant influence on both pelagic respiration and surface CO_2 fluxes of lakes within the watershed. Lakes in recently burnt watersheds had both higher respiration and CO_2 fluxes, even after the influence of lake and watershed size was accounted for. Previous studies have reported mixed results concerning the influence of fire on lake function: Some have described transient postfire increases in nutrient loading to lakes (Wright, 1976) and streams (Bayley *et al.*, 1992), and lake morphometry, drainage ratio, water residence time, trophic status and relative concentrations of nutrients

are important in mediating these fire-induced effects (Carignan & Steedman, 2000). Other studies have reported no measurable changes in DOC, TN and TP in runoff from recently burnt areas (Lewis, 1974; Richter *et al.*, 1982). Our own analyses did not reveal significant differences in lake trophic status (TP, TN, Chl a), DOC concentrations, or DOC quality (as specific absorbance $\text{ABS}_{440}/\text{DOC}$), related to watershed type in terms of fire history. Overall, the underlying basis for the effect of fire on lake C metabolism and flux is unclear, either because the effect is below the natural background noise of the variables the variables that we measured, or more likely because it was exerted through variables that we did not cover.

In this boreal region, the frequency of fire determines the distribution of stands of different age in the landscape and the subsequent differences in net ecosystem production, and soil C accumulation and soil properties (Litvak *et al.*, 2003). These features in turn influence the amount and nature of the materials exported from the watershed (Neff & Hooper, 2002). Fire further influences soil biogeochemistry (see Certini, 2005 for a review), and soil metabolism (Amiro, 2001; Czimeczik *et al.*, 2006), which in turn may translate into shifts in both the amounts and nature of materials exported to lakes (Essington & Carpenter, 2000). Other, long-term effects of fire may be exerted through its influence on local hydrological and micro-meteorological features, but we have no hydrological data, and our own *in situ* measurements of wind speed taken in these lakes show no significant relationship to YAF, so this question needs to be further explored. Regardless of the origin of these effects, the correlation that we found between CO_2 flux and pelagic respiration would suggest that these watershed influences on C emissions might be mediated at least in part by impacts on lake C metabolism, in turn suggesting a fire-induced shift in the organic C pool available to microbial utilization in lakes. This conclusion is further strengthened by the positive relationship between BP and respiration, and the lack of any relationship between respiration and nutrients or chlorophyll, which would suggest that bacterial metabolism supported by DOC is a large component of total respiration in these boreal lakes.

The differences in fluxes due to fire history in the watershed are not trivial: For example, if we take a lake of 1 km^2 (close to the median lake surface in the region), with a watershed of 7 km^2 (average ratio of lake to basin area in the region is 6.7), the predicted CO_2 fluxes [using Eqn (6)] would be in the order of $29 \text{ mg C m}^{-2} \text{ day}^{-1}$ if the watershed was burnt 30 years ago, and over $90 \text{ mg C m}^{-2} \text{ day}^{-1}$ if the watershed was burnt 5 years

ago. Calculated over the ice-free period, these differences in flux would amount to a minimum of 13 tons C yr⁻¹ emitted in excess by the lake lying in the recently burnt watershed relative to the same size lake in an unburnt watershed. Scaled to the entire watershed, this fire-induced aquatic CO₂ flux would be in the order of 2–3 g C m⁻² (of burnt watershed) yr⁻¹, which is locally significant since it is similar, for example, to the long-term C accumulation in soils in this region (2–3 g C m⁻² yr⁻¹, Roehm *et al.*, 2009), and of the same magnitude as the DOC export from boreal catchments (Dillon & Molot, 1997; Jonsson *et al.*, 2003). At the regional scale, fire affects approximately 0.5–1% of the landscape per year in this region of Québec (Bergeron *et al.*, 2001), so that at any given time at least 5–10% of the landscape, and the lakes therein, have been affected by a relatively recent (<10 years) fire. A first-order estimate of fire-induced aquatic C emissions over the entire landscape would thus range between 0.1 and 0.3 g C m⁻² yr⁻¹, which represents 2–3% of current estimates of direct C emissions from forest fires in boreal regions (around 9 g C m⁻² yr⁻¹, Bachelet *et al.*, 2005). This estimate is conservative because this boreal landscape is a complex mosaic of patches of different fire ages, and these fire-induced aquatic fluxes are not one-time events but must rather be integrated over time, so that the overall impact on the regional C balance is likely to be larger.

Climate, forest fire frequency, and the boreal C cycle

Warming, along with higher maximum temperatures and increased droughts could potentially accelerate fire cycles in terms of frequency and intensity, both of which play key roles in shaping the postfire successional pattern in the boreal region (Arsenault 2001). In this regard, retrospective studies have detected significant increases in the frequency of fire in Northern landscapes, particularly in the past century (Kurz & Apps, 1999; Flannigan *et al.*, 2001). The current prediction for Northern regions as a whole is a 50% increase in fire occurrence in parts of the circumboreal by the end of this century (Flannigan *et al.*, 2008), with a doubling of the area burnt per decade by 2041–2050, and an increase on the order of 3.5–5.5 times by the last decade of the 21st century (Balshi *et al.*, 2008). Zhuang *et al.* (2002) have further suggested that boreal forests could become net sources of CO₂ if fire frequency exceeds a certain threshold. There is a large regional variability in these trends, and for example, there is indication that in South- and Central-Eastern boreal region of Québec (which includes our study area) fire cycles have in fact been longer since the end of the Little Ice Age (~1850), and that this trend will continue (Bergeron *et al.*, 2001),

with an subsequent increase in the proportion of old-growth forests (>100 years old) in the landscape (Lesieur *et al.*, 2002). Regardless of whether the frequency and intensity of fire may decrease or increase locally in the future, our results suggest that these shifts will impact lake C emissions. In the case of North-Eastern Québec, overall lake CO₂ emissions should decline where the extent of old growth forest increases as a result of lower forest fire frequencies. However, increases in fire frequency and intensity, predicted for much of the circumboreal region, should result in significantly increased overall aquatic C emissions during the coming decades.

The obvious and immediate consequence of fire is the rapid return to the atmosphere of C that was stored in plant biomass, a process that is of great significance globally (van der Werf *et al.*, 2004). More subtle effects of fire involve the long-term increase in the loss of terrestrial C to the atmosphere through enhanced postfire soil export and respiration, a process that has only recently been addressed (i.e. Bergner *et al.*, 2004; Certini, 2005). Harden *et al.* (2002) have suggested, based on an analysis of C stocks and terrestrial primary production that the long-term C emission due to fire in the boreal landscape has been greatly underestimated in global C cycle models. The fire-induced enhancement of lake organic C mineralization and C emissions represents yet another long-term effect, which increases the overall C loss from the landscape as the result of fire and that have not been included in any regional models or budgets. There is little question that climate change will influence boreal lake C metabolism through the direct effects of the (predicted) increases in average water temperatures, and also through indirect effects on the regional hydrology, soil properties and the movement of materials within watersheds (Sobek *et al.*, 2003). Our results suggest that climate change may further influence lake C metabolism and greenhouse gas dynamics indirectly through its control of fire frequency and severity, therefore establishing yet another positive feedback between climatic and biogeochemical processes in the landscape, which needs to be considered.

Acknowledgements

This research was supported financially and logistically by Hydro-Québec, through the Hydro-Québec/UQÀM Eastmain-1 Research project. We especially thank A. Tremblay (Hydro-Québec) for his continuing support to this project. We would also like to thank Charlotte Roehm, Annick St. Pierre, Martine Camire and Simon Barette, for field assistance, and Catherine Beauchemin for laboratory analysis. D. M. was supported by a NSERC Graduate Scholarship.

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