

Diurnal sampling reveals significant variation in CO₂ emission from a tropical productive lake

Reis, PCJ.^{a*} and Barbosa, FAR.^a

^aLaboratório de Limnologia, Ecotoxicologia e Ecologia Aquática – LIMNEA, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais – UFMG, Av. Antônio Carlos, 6627, Pampulha, CEP 30161-970, Belo Horizonte, MG, Brazil

*e-mail: paulacjr@gmail.com

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Abstract

It is well accepted in the literature that lakes are generally net heterotrophic and supersaturated with CO₂ because they receive allochthonous carbon inputs. However, autotrophy and CO₂ undersaturation may happen for at least part of the time, especially in productive lakes. Since diurnal scale is particularly important to tropical lakes dynamics, we evaluated diurnal changes in *p*CO₂ and CO₂ flux across the air-water interface in a tropical productive lake in southeastern Brazil (Lake Carioca) over two consecutive days. Both *p*CO₂ and CO₂ flux were significantly different between day (9:00 to 17:00) and night (21:00 to 5:00) confirming the importance of this scale for CO₂ dynamics in tropical lakes. Net heterotrophy and CO₂ outgassing from the lake were registered only at night, while significant CO₂ emission did not happen during the day. Dissolved oxygen concentration and temperature trends over the diurnal cycle indicated the dependence of CO₂ dynamics on lake metabolism (respiration and photosynthesis). This study indicates the importance of considering the diurnal scale when examining CO₂ emissions from tropical lakes.

Keywords: *p*CO₂, CO₂ flux, diurnal variations, tropical productive lake.

Amostragem diurna demonstra variação significativa na emissão de CO₂ em um lago tropical produtivo

Resumo

É amplamente aceito na literatura que lagos são em geral heterotróficos e supersaturados com CO₂ já que recebem carbono alóctone. Porém, autotrofia e insaturação de CO₂ podem ocorrer em pelo menos parte do tempo, especialmente em lagos produtivos. Como a escala diurna é particularmente importante para a dinâmica de lagos tropicais, variações diurnas na *p*CO₂ e no fluxo de CO₂ através da interface ar-água foram avaliadas num lago tropical produtivo do sudeste do Brasil (Lagoa Carioca) durante dois dias consecutivos. Tanto a *p*CO₂ quanto o fluxo de CO₂ foram significativamente diferentes entre o dia (9:00 às 17:00) e a noite (21:00 às 5:00), confirmando a influência desta escala na dinâmica do CO₂ na Lagoa Carioca. Foram registradas heterotrofia e emissão de CO₂ pela lagoa apenas durante a noite, enquanto durante o dia não houve emissão significativa. Variações na concentração de oxigênio dissolvido e na temperatura ao longo do dia indicaram a dependência da dinâmica do CO₂ no metabolismo (respiração e fotossíntese) deste lago. Este estudo indica a importância de se considerar a escala diurna na avaliação da emissão de CO₂ por lagos tropicais.

Palavras-chave: *p*CO₂, fluxo de CO₂, variações diurnas, lago tropical produtivo.

1. Introduction

It is widely accepted that lakes are typically supersaturated with CO₂ relative to the overlying atmosphere (Kling et al., 1991; Cole et al., 1994; Duarte and Prairie, 2005). This net heterotrophic condition is believed to predominate as ecosystem respiration frequently exceeds ecosystem primary production in lakes due to the input of allochthonous organic matter from their catchments (Del Giorgio et al., 1999; Pace et al., 2004). However, recent studies have shown that although heterotrophy is frequent it is not a general rule. CO₂ undersaturation and/or autotrophy

have been recorded in lakes, especially on those with high production rates (e.g. Xing et al., 2005; Gu et al., 2011; Laas et al., 2012). Productive lakes support lower respiration rates than the unproductive ones and then tend to be net CO₂ sinks (Duarte and Agustí, 1998). Besides lake productivity, other factors are thought to influence the metabolism and partial pressure of CO₂ (*p*CO₂) in the surface waters of lakes, such as temperature, dissolved organic carbon concentration, and dissolved inorganic carbon inputs from the watershed (e.g. Hanson et al.,

2003; Johnson et al., 2008; Kosten et al., 2010). Lake's $p\text{CO}_2$ is then the result of the interaction of many factors and the extent to which each factor controls CO_2 likely varies among systems and across time scales.

Many studies in boreal and temperate regions have tested the prevalence of CO_2 supersaturation in lakes (e.g. Riera et al., 1999; Tank et al., 2009; Huotari et al., 2009); however, much less is known about CO_2 emissions from tropical lakes (e.g. Richey et al., 2002; Marotta et al., 2009; Kosten et al., 2010; Belger et al., 2011). Knowing precisely how much carbon is delivered to the atmosphere by tropical inland waters and understanding the regulation of this process are crucial steps for better assessment of regional and global carbon budgets.

Diurnal changes in temperature and irradiance may be very large in tropical lakes (e.g. Barbosa and Tundisi, 1989a). Compared to boreal and temperate regions, seasonal variations on temperature and photoperiod are small in the tropics (e.g. Barbosa, 1997) while temperature variations within a day can be just as large or even exceed temperature differences between seasons. In tropical lakes, diurnal changes in temperature can be large enough to cause water mixing at night, a pattern described by Lewis (1973) in Lake Lanao as *atelmixis* and more recently re-described in two Brazilian lakes by Barbosa and Padisák (2002). Metabolic processes may also vary widely over the course of the day, as demonstrated for phytoplankton (Barbosa and Tundisi, 1989b) and bacterioplankton production (Petrucio and Barbosa, 2004). Since diurnal changes are large in the tropics and productive lakes are more likely to be autotrophic (Duarte and Agusti, 1998), it is possible that tropical productive lakes show significant metabolism and CO_2 variations over the course of the day, including diurnal changes between heterotrophy and autotrophy.

In this context, the goal of this study was to check for significant variations within a day in surface water CO_2 partial pressure ($p\text{CO}_2$) and CO_2 fluxes between lake and atmosphere in a tropical productive lake (Lake Carioca).

2. Material and Methods

2.1. Site description

Lake Carioca (19°45'26.0"S; 42°37'06.2"W) is located in the Rio Doce State Park (Parque Estadual do Rio Doce, PERD; Figure 1) in an Atlantic Forest remnant in Minas Gerais, Brazil. The park is part of the middle Rio Doce Lacustrine System, which consists of more than two hundred lakes and ponds of varying size, morphometry and trophic state. Roughly 51 lakes are inside PERD, including Lake Carioca, and thus protected from direct human impacts. However, PERD is surrounded by agriculture, pasturelands, and large areas of *Eucalyptus* spp plantations that have considerable impacts on the lacustrine system and the forest of the park. Carioca is a small (0.14 km²) shallow lake (max. depth = 11.8 m, Bezerra-Neto et al., 2010) and exhibits high production rates (annual average of 497 mgC.m⁻².d⁻¹, PELD Technical Report, unpublished data). It mixes vertically once a year during the dry season (between May and August), when primary production is boosted by nutrients from the hypolimnium of the lake.

2.2. Sampling and calculations

Samples were collected at the end of the dry season (August, 2011) just after the water mixing and at the beginning of thermal stratification. Basic limnological data including water temperature, pH, conductivity and dissolved oxygen (D.O.) were taken at the deepest point of the lake with a Hydrolab DS 5 (Hydromet Inc.) probe at depth intervals of 0.5 m. Water samples for analysis of nutrients and chlorophyll-*a* determination were collected at 4 depths corresponding to 100%, 10% and 1% of surface irradiance, as well as the aphotic zone (defined with a 1400 series International Light Technologies radiometer). These data are not discussed in detail herein and are provided as background information only.

Surface water CO_2 partial pressure ($p\text{CO}_2$) and CO_2 flux across the air-water interface were measured every 4 hours at the deepest point of Lake Carioca over two diurnal cycles. Direct measurements of $p\text{CO}_2$ were taken by headspace equilibration according to Cole and Caraco (1998) with modification. Three 30 mL glass bottles (triplicates) were filled with 20 mL of lake surface water (0.5 m depth) and immediately capped and sealed with rubber and metal caps. Ten mL of ambient air was introduced to each bottle with a syringe and needle through the rubber cap. The bottles were then shaken vigorously for 60 seconds to allow for equilibration of the air and water phases for CO_2 . Headspace air was collected with a syringe and injected in an infrared gas analyser (IRGA) (environmental gas monitor EDSEGM4; PP-Systems, Hitchin, Hertfordshire) for $p\text{CO}_2$ measurement. $p\text{CO}_2$ of ambient air ($p\text{CO}_{2\text{air}}$) was also measured by the IRGA. Surface water CO_2 concentration (C_{sur}) and the saturation concentration of CO_2 (C_{sat}) were calculated from measured $p\text{CO}_2$ s and Henry's constant at ambient temperature (K_{H}) according to Henry's law (Weiss, 1974) (Equation 1 and 2):

$$C_{\text{sur}} = p\text{CO}_{2\text{water}} K_{\text{H}} \quad (1)$$

$$C_{\text{sat}} = p\text{CO}_{2\text{air}} K_{\text{H}} \quad (2)$$

CO_2 fluxes across air-water were estimated using the following equation according to Cole and Caraco (1998) (Equation 3):

$$\text{Flux} = \alpha k (C_{\text{sur}} - C_{\text{sat}}) \quad (3)$$

where α is the factor for chemical enhancement of diffusion (Wanninkhof and Knox, 1996) and k is the coefficient of gas exchange for CO_2 at a given temperature. k was calculated from k_{600} for low wind speeds (Equation 4) (Cole and Caraco, 1998) and from Schmidt numbers ratio (Equation 5) (Jähne et al., 1987):

$$k_{600} = 2.07 + 0.215 U_{10}^{1.7} \quad (4)$$

$$k = k_{600} (\text{Sc} / 600)^{-0.67} \quad (5)$$

U_{10} is wind speed at 10 m and was estimated with the Smith (1985) equation using measured wind speed at 1 m by an anemometer at the centre of the lake. Sc is the in situ Schmidt number for CO_2 (Jähne et al., 1987).



Figure 1. Rio Doce State Park in southeast Brazil. The circle shows Lake Carioca. Source: Adapted from IBGE/Brasil topographical map by Philippe Maillard – Institute of GeoSciences-IGC, Federal University of Minas Gerais.

Continuous measurements of dissolved oxygen concentration were taken by an automated sensor (D-Opto Logger, Zebra-Tech Ltd.) deployed in the centre of the lake at 0.5 m depth.

2.3. Statistical analysis

T-tests were used to check for differences in surface water *p*CO₂ between day and night and to check for differences between surface water *p*CO₂ and *p*CO₂ in

the overlying atmosphere. All tests were performed in Statistica 7.0 software.

3. Results

Limnological conditions of Lake Carioca in August (2011) are summarised in Table 1. Water temperature ranged from 21.4 °C at the bottom to 23.6 °C at the surface, showing the beginning of thermal stratification. The lake

Table 1. Limnological data at selected depths in Lake Carioca during the dry season (August, 2011).

Depth (m) Variables	0	1.5	4.5	8
Water temperature(°C)	23.6	22.8	21.8	21.4
pH	8.03	8.06	6.32	6.14
Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	28	28	29	41
D.O. ($\text{mg}\cdot\text{L}^{-1}$)	12.7	12.8	4.4	0.1
Alk. ($\text{meqCO}_2\cdot\text{L}^{-1}$)	0.26	0.24	0.32	0.35
Chl- <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	49.2	58.8	105.3	57.7
Primary Productivity ($\text{mgC}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$)	10.1	12.0	5.7	0
PO_4^{-3} ($\mu\text{g}\cdot\text{L}^{-1}$)	2.0	1.5	1.1	0.7
P_{total} ($\mu\text{g}\cdot\text{L}^{-1}$)	14.6	23.4	16.8	18.4
NH_4^{+} ($\mu\text{g}\cdot\text{L}^{-1}$)	11.5	9.1	87.4	347.2
NO_2^{-} ($\mu\text{g}\cdot\text{L}^{-1}$)	0.5	0.6	0.3	0.4
NO_3^{-} ($\mu\text{g}\cdot\text{L}^{-1}$)	5.2	4.3	3.2	0.3
N_{total} ($\mu\text{g}\cdot\text{L}^{-1}$)	873.7	837.6	931.0	724.9
SiO_2 ($\text{mg}\cdot\text{L}^{-1}$)	0.4	0.6	0.3	0.4

exhibited a well-developed oxycline at approximately 4 m and an anoxic hypolimnium. The water was alkaline (pH *c.* 8) down to 4.5 m but pH decreased to *c.* 6 at the lower layers. The dissolved oxygen and pH profiles indicated high respiration rates and CO_2 concentrations at the bottom of the lake.

Surface water $p\text{CO}_2$ ($p\text{CO}_{2\text{water}}$) ranged considerably (from 389.7 to 643.3 μatm) in Lake Carioca during the sampling period and had a mean value of 488.8 ± 78.6 μatm . Mean night $p\text{CO}_{2\text{water}}$ (565 $\mu\text{atm} \pm 55.3$ (\pm SD) from 21:00 to 5:00) was significantly higher than mean day $p\text{CO}_{2\text{water}}$ (436.1 $\mu\text{atm} \pm 25.5$ (\pm SD) from 9:00 to 17:00) ($t = -8.14$; d.f. = 15; $p < 0.001$, Figure 2), showing significant changes in the CO_2 dynamics of this lake within a day. A strong metabolic control of lake's CO_2 was evidenced by the similar but opposite trends of dissolved CO_2 and O_2 over the diurnal cycle (Figure 3A). As expected, during daytime photosynthesis lowered water $p\text{CO}_2$ and raised dissolved oxygen (D.O.) concentration. At night, when just respiration occurs, $p\text{CO}_2$ increased considerably and the concentration of D.O. in the water reduced (Figure 3A). Diurnal variations in water temperature also showed opposite trend to CO_2 with increases during the day and decreases at night (Figure 3B). These mirror-like trends indicate that respiration and photosynthesis are major regulators of CO_2 dynamics in Lake Carioca. However, small differences between CO_2 and O_2 variations suggest that other factors may also have some influence on the lake's CO_2 concentration.

Mean $p\text{CO}_{2\text{water}}$ was significantly higher than mean $p\text{CO}_2$ in the overlying atmosphere ($p\text{CO}_{2\text{air}}$) during nighttime (from 21:00 to 5:00; $t = 4.34$, g.l. = 30; $p = 0.0001$) but were not significantly different during daytime (from 9:00 to 17:00; $t = 1.68$, g.l. = 29.8; $p = 0.10$) (Figure 4). This means that Lake Carioca alternated between CO_2 supersaturation and atmospheric equilibrium within 24 hours and therefore, the lake was not always a source of CO_2 but only during nighttime (Figure 5). Even at night,

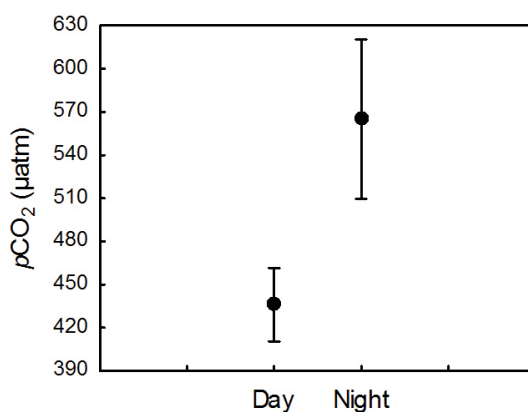


Figure 2. Mean (\pm SD, $n=16$) $p\text{CO}_2$ (μatm) in Lake Carioca surface water during day and night. $p < 0.001$ indicating significant difference (t -test).

CO_2 emission from Lake Carioca was low, showing a maximum of 2.4 $\text{mmolCO}_2\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ at 1:00 of the first day (Figure 5). Mean CO_2 flux throughout the studied period was only 0.9 $\text{mmolCO}_2\cdot\text{m}^{-2}\cdot\text{d}^{-1} \pm 0.8$ (\pm SD). Low values of CO_2 efflux from Lake Carioca are consequences of the relatively low $p\text{CO}_2$ in its water and almost null wind speeds registered during the sampling period.

4. Discussion

Our results bring to light significant diurnal changes in $p\text{CO}_{2\text{water}}$ and CO_2 emissions from a productive tropical lake. The use of the diurnal approach demonstrated that despite the belief that lakes are generally net heterotrophic and supersaturated with CO_2 , Lake Carioca was not a constant source of CO_2 and was heterotrophic only during the night.

Diurnal dynamics of CO_2 have been recorded in temperate lakes (e.g. Sellers et al., 1995; Cole and Caraco, 1998; Hanson et al., 2006) but generally showed small

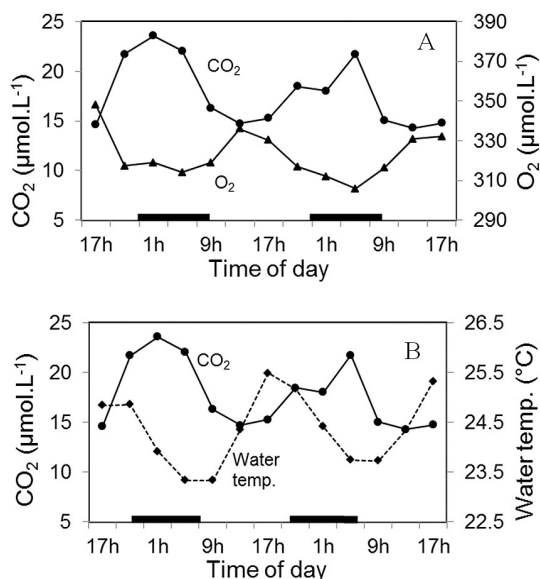


Figure 3. A. Concentrations of dissolved CO₂ and O₂ in the surface water. B. Concentration of dissolved CO₂ and surface water temperature. All variables were measured at 4-hour intervals over a 48-hour cycle on Lake Carioca in August, 2011. Horizontal bars mean nighttime hours.

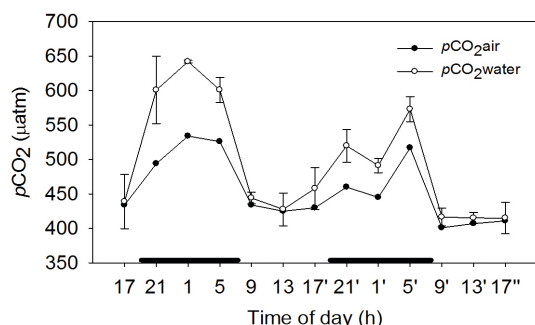


Figure 4. Mean (±SD) pCO₂ in the water (pCO₂_{water}) and in the overlying atmosphere (pCO₂_{air}) measured at 4-hour intervals over a 48-hour cycle on Lake Carioca in August, 2011. Horizontal bars mean nighttime hours.

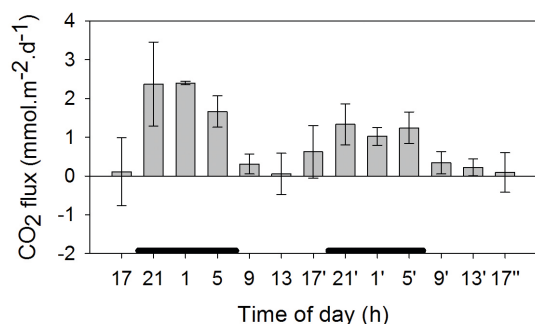


Figure 5. Mean (±SD) CO₂ flux across the air-water interface of Lake Carioca, measured at 4-hour intervals over a 48-hour cycle in August, 2011. Positive values indicate that CO₂ flux was towards atmosphere and negative values indicate CO₂ flux towards the water. Horizontal bars mean nighttime hours.

variation. Cole and Caraco (1998) for instance, recorded small CO₂ changes within a day in midsummer and even smaller ones during the spring in Mirror Lake. Differently, the significant variation between day and night in CO₂ dynamics recorded for the tropical and productive Lake Carioca-southeast Brazil can be explained by large metabolic differences between periods of the day, which is not pronounced on higher latitude and/or unproductive lakes. As shown here, in productive and warm lakes, gross primary production can be high enough to equilibrate or eventually exceed respiration rates during daytime. Moreover, although this study was conducted only during the dry season, it is likely that diurnal variation in pCO₂ in Lake Carioca is even larger during the rainy season. The higher mean temperature and greater input of nutrients and dissolved organic carbon from the watershed during the rainy season (summer) might favour both autotrophy and heterotrophy in the lake (Brown et al., 2004; Staehr and Sand-Jensen, 2007; Marotta et al., 2012) likely resulting in higher amplitude of diurnal CO₂ variations (Marotta et al., 2010).

Surface water pCO₂ registered in Lake Carioca is very low in comparison to the mean pCO₂ for tropical lakes available in the published literature (1804 matm, Marotta et al., 2009). Also differently from what was found by other studies that covered tropical lakes (e.g. Cole et al., 1994; Marotta et al., 2009), Lake Carioca is a small source of atmospheric carbon in comparison to higher latitude lakes. While CO₂ emissions from Lake Carioca averaged only 0.9 mmolCO₂.m⁻².d⁻¹, other studies have recorded CO₂ effluxes of 20.9 mmolCO₂.m⁻².d⁻¹ from Arctic lakes (Kling et al., 1991), 55.6 mmolCO₂.m⁻².d⁻¹ from a boreal humic lake (Huotari et al., 2009), and 1200 and 90 mmolCO₂.m⁻².d⁻¹ from two clear-water temperate lakes (Riera et al., 1999). The registered low values of pCO₂ and CO₂ efflux from Lake Carioca are probably a consequence of its high autotrophic activity, particularly during the studied period when vertical mixing induces high production rates (640 mgC.m⁻².d⁻¹; PELD Report, 2012) and scarce rainfall limits the input of allochthonous dissolved organic carbon to the lake likely reducing its respiration rates (Cole et al., 2000). Moreover, the lack of rainfall can also lead to lower values of pCO₂ in Lake Carioca in the dry season than in the rainy season since rainfall can enhance CO₂ inputs from groundwater to lakes (Marotta et al., 2010).

As shown in this study, diurnal changes in CO₂ can be significant in tropical waters and ignoring this variation may render misvaluations and misconclusions of the role of tropical aquatic ecosystems in the global carbon cycle. Such conclusions bring new possibilities for further studies concerning the general acceptance of a predominant heterotrophy of lakes, and highlight potential temporal changes between net autotrophy and net heterotrophy in lakes, especially in the tropical and productive ones where temperature and nutrients maintain high autochthonous production rates.

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Erratum

Due to a formatting error in the article “Diurnal sampling reveals significant variation in CO₂ emission from a tropical productive lake” published in volume 74, issue 3 (suppl.), p. 113-119, in the page 116, first column, lines 8, 10 and 12 and in the page 117, second column, line 24 where you read “matm”, you should read “μatm”.