

The role played by aquatic macrophytes regarding CO₂ balance in a tropical coastal lagoon (Cabiúnas Lagoon, Macaé, RJ)

O papel desempenhado pelas macrófitas aquáticas em relação ao balanço de CO₂ em uma lagoa costeira tropical (Lagoa Cabiúnas, Macaé, RJ)

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Abstract: Aim: Carbon dioxide (CO₂) is an important atmospheric trace gas that is involved in both the biological carbon cycle and global warming. Inland waters - mainly lakes - contribute to C cycling and have been considered a large source of atmospheric CO₂. However, scientific studies usually neglect lake morphometry and the presence of aquatic macrophytes in littoral zones, which have a great potential for CO₂ absorption and for C storage. This study aimed to evaluate the importance of the littoral region on the CO₂ balance in the Cabiúnas Lagoon, while also considering the contribution of the limnetic region and of *Typha domingensis* and *Eichhornia azurea*, prominent species in the area. **Methods:** CO₂ flux was estimated by a linear integration of CO₂ concentrations measured in the internal atmospheric of a single-component static closed chambers at the studied sites. The distribution of macrophyte stands throughout lagoon surface was taken into account to evaluate the effects of macrophytes on CO₂ supersaturation. Other factors were also measured throughout the sampling process to evaluate their relationship with CO₂ flux data by means of Akaike model selection criterion. The area covered by aquatic macrophytes at the Cabiúnas lagoon was estimated by profiles and transects. **Results and discussion:** CO₂ flux through the water surface ranged from -7.39 to 17.56 mgCO₂m⁻²h⁻¹. An emission pattern predominated, suggesting that water columns are CO₂ supersaturated at all sampling sites. Rates were similar among all the sampling sites, suggesting that aquatic macrophytes do not influence CO₂ saturation in the water column at Cabiúnas lagoon. On the other hand, CO₂ fluxes from macrophyte tissues showed a clear assimilation pattern. Influxes were higher in *T. domingensis* (-229.1 ± 320.9 mg CO₂.m⁻².h⁻¹) than in *E. azurea* stands (-43.8 ± 39.5 mg CO₂.m⁻².h⁻¹). Once these macrophytes covered a considerable area of the lagoon and CO₂ absorption strongly overwhelmed the emission processes, then we were able to extrapolate data from the total estimated area of the evaluated sites (75% of the Cabiúnas lagoon), which resulted in a net influx of 46.6 mg CO₂.m⁻².h⁻¹. The strong *Typha domingensis* contribution to CO₂ absorption and other C cycling processes indicate that it is one of the most important species to Carbon cycling in the studied ecosystem. Thus, it is worth considering C cycling in lake littoral zones as a key process when estimating C balance in shallow aquatic ecosystems.

Keywords: carbon cycling, *Typha domingensis*, littoral zone, shallow lakes.

Resumo: Objetivo: O dióxido de carbono (CO₂) é um importante gás atmosférico envolvido tanto no ciclo biológico do carbono como no aquecimento global. Corpos d'água continentais - principalmente lagos - contribuem para o ciclo do carbono e têm sido considerados uma grande fonte de CO₂ para atmosfera. No entanto, estudos científicos geralmente negligenciam a morfometria dos lagos e a presença de macrófitas aquáticas na região litorânea destes ecossistemas, que possuem um grande potencial tanto para a absorção de CO₂ como para o estoque de carbono. Este estudo teve como objetivo avaliar a importância das regiões litorânea - considerando a contribuição das espécies dominantes *Typha domingensis* e *Eichhornia azurea* - no balanço de CO₂ na Lagoa Cabiúnas, contrastando com a região limnética. **Métodos:** O fluxo de CO₂ foi estimado por meio de regressões lineares das concentrações de CO₂ na atmosfera interna de câmaras estáticas,

em cada um dos locais estudados. Foi verificada a distribuição de macrófitas ao longo do espelho d'água para avaliar os efeitos desta comunidade sobre a saturação de CO_2 . Outras variáveis também foram medidas ao longo do processo de amostragem para avaliar a sua relação com os dados de fluxo de CO_2 por meio de critérios de seleção de modelos de Akaike. A área coberta por macrófitas aquáticas na lagoa Cabiúnas foi estimada por perfis e transectos. **Resultados e discussão:** O fluxo de CO_2 na superfície da água variou entre $-7,39$ a $17,56 \text{ mgCO}_2\text{m}^{-2}\text{h}^{-1}$. Foi observado predominantemente um padrão de emissão de CO_2 pela superfície d'água sem macrófitas, sugerindo que a coluna d'água encontra-se supersaturada de CO_2 como um todo. Os valores foram semelhantes entre todos os pontos de amostragem, sugerindo que as macrófitas aquáticas não influenciam na saturação de CO_2 na coluna d'água da lagoa Cabiúnas. Por outro lado, os fluxos de CO_2 a partir do tecido das macrófitas mostrou um padrão claro de absorção. Influxos foram maiores em *T. domingensis* ($-229,1 \pm 320,9 \text{ mg CO}_2\text{m}^{-2}\text{h}^{-1}$) do que em *E. azurea* ($-43,8 \pm 39,5 \text{ mg CO}_2\text{m}^{-2}\text{h}^{-1}$). Uma vez que estas macrófitas ocupam uma área considerável da lagoa (75% da lagoa Cabiúnas) e o balanço de CO_2 aponta para predominância de processos de absorção do gás, isso resulta num aporte líquido de $46,6 \text{ mg CO}_2\text{m}^{-2}\text{h}^{-1}$ a lagoa Cabiúnas. A elevada contribuição de *Typha domingensis* para absorção de CO_2 e em outros processos apontam esta espécie como uma das mais importantes para a ciclagem do C neste ecossistema. Assim, a contribuição da região litorânea não pode ser negligenciada nas estimativas do balanço de C nos ecossistemas aquáticos rasos.

Palavras-chave: ciclagem do carbono, *Typha domingensis*, região litorânea, lagos rasos.

1. Introduction

Carbon dioxide (CO_2) is an important atmospheric trace gas that is closely interconnected to the biological carbon cycle. The heat-absorbing properties of CO_2 increase the atmosphere's warming potential and make CO_2 a key radiatively active greenhouse gas (GHG), contributing to global warming (IPCC, 2007). In this context, recent studies showed that inland water, like lakes, streams and wetlands, plays a significant role in the global carbon (C) cycle when compared to terrestrial and marine environments (Battin et al., 2009). Among such aquatic systems, lakes have been extensively considered as great CO_2 sources to the atmosphere. Such recognition emerged from a series of surveys based on carbon dioxide partial pressure (pCO_2) over water surfaces, encompassing a large number of systems worldwide (Cole et al. 1994; Sobek et al. 2005; Marotta et al. 2009). The net CO_2 flux from these lake surfaces into the atmosphere depict that the water column in these ecosystems are CO_2 supersaturated. Therefore, lakes are considered net heterotrophic ecosystems (del Giorgio et al. 1999), meaning that, organic carbon mineralization by heterotrophic organisms, exceeds CO_2 fixation by the phototrophic ones.

The processes determining CO_2 production and emission, as well as CO_2 saturation in aquatic ecosystems, may differ due to organic matter (OM) input and are regulated by factors such as oxygen availability, organic matter availability and composition, sediment and water temperature

and chemistry, the presence of electron acceptors (redox conditions), pH, electrical conductivity (EC) and factors such as water depth and lake size (e.g., Casper et al., 2003, Stadmark and Leonardson, 2005; Frei et al., 2006; Repo et al., 2007; Loeb et al., 2007; Juutinen et al., 2009). As is observed in tropical lakes, some ecosystems can show CO_2 supersaturation for days or even for years (Marotta et al., 2009).

So far, studies concerning CO_2 emissions from lakes have been based in measurements performed basically at the limnetic compartment. However, most lakes have a high proportion of shoreline in relation to area and volume (Downing et al., 2006), so their littoral zones are very important to ecosystem dynamics (Panosso et al., 1998). Among these small aquatic ecosystems, shallow coastal lagoons are the most prevalent in Brazil (Esteves, 2011). These ecosystems allow large aquatic macrophytes to establish in their relatively extensive littoral zone. Aquatic macrophytes comprise several different functional groups: emergent, floating-leaved, floating or submersed (Wetzel, 1983; Esteves, 1998). Functional groups differ in their chemical composition and, consequently, in their stoichiometric ratios. In turn, macrophytes influence the metabolic functions in aquatic systems, such as nutrient stocking and cycling (Santos et al., 2006; Suhett et al., 2007).

It has been shown that macrophytes significantly influence trace gas exchange due to their influence over C production, consumption and transport processes (Nobel, 1983; Laanbroek, 2010). Gas

transportation to and from the canopy results from turbulent mixing, whereas migration across leaf boundary layers occurs by means of molecular diffusion or mass flow governed by stomatal and cuticular conductance (Nobel, 1983; Jarvis and McNaughton, 1986). Plants may affect trace gas production or consumption by altering the rhizosphere's physical and chemical environment, by hosting microbial communities, by uptaking or releasing resources to soil microbial communities (Matson et al., 1990) or by leaf exchange and the metabolism of gases above the surface (Lamb et al., 1987; Denmead, 2008). Therefore, macrophyte-dominated areas must be considered to understand the CO₂ dynamics within aquatic ecosystems and the role it plays in CO₂ flux into the atmosphere.

The present study intended to evaluate the littoral region's importance to CO₂ balance in the Cabiúnas Lagoon, as an atmosphere C dissipater or source, due to the presence of aquatic macrophytes. Concerning the CO₂ dynamics in coastal aquatic ecosystems, studies performed at the same system showed that it tends to be a consistent CO₂ source to the atmosphere (Marotta et al., 2009; 2010). However, these studies did not evaluate the role of aquatic macrophytes gas transportation and alterations in the littoral zone to CO₂ dynamics. Therefore, we aimed to compare the limnetic contributions to areas dominated by *Typha domingensis* Pers. and *Eichhornia azurea* (SW.) Kunth in the littoral region regarding CO₂ fluxes between lake and atmosphere.

2. Material and Methods

2.1. Study site

The study was performed in the Cabiúnas Lagoon (22° 24' S, 41° 42' W), located in the Restinga de Jurubatiba National Park in the state of Rio de Janeiro, Brazil (Figure 1). The region presents a humid/mesothermic climate, with small temperature variations throughout the year. The mean annual precipitation rate is 1300 mm, with higher rainfall in the spring and summer. Mean annual temperature is 22 °C and the mean temperature in the summer reaches 25 °C (Panosso et al., 1998). Cabiúnas is a pristine freshwater coastal lagoon surrounded by a natural restinga ecosystem featuring coarse sandy soil. The highly permeable watershed and dendritic morphometry (Figure 1) of the Cabiúnas favors a large input of colored terrestrial dissolved organic matter into the lagoon (Caliman et al., 2010), contributing to its waters' classification as humic. Cabiúnas' shallow water column and dendritic morphometry support the establishment and the growth of aquatic macrophytes on its margins (Panosso et al., 1998).

At the Cabiúnas Lagoon, homogeneous stands of *Typha domingensis* and *Eichhornia azurea* are distributed in a depth gradient. Stands of the emergent macrophyte *T. domingensis* dominate the water-land interface, and stands of the floating-leaved *E. azurea* dominate the interface between the littoral and the limnetic region.

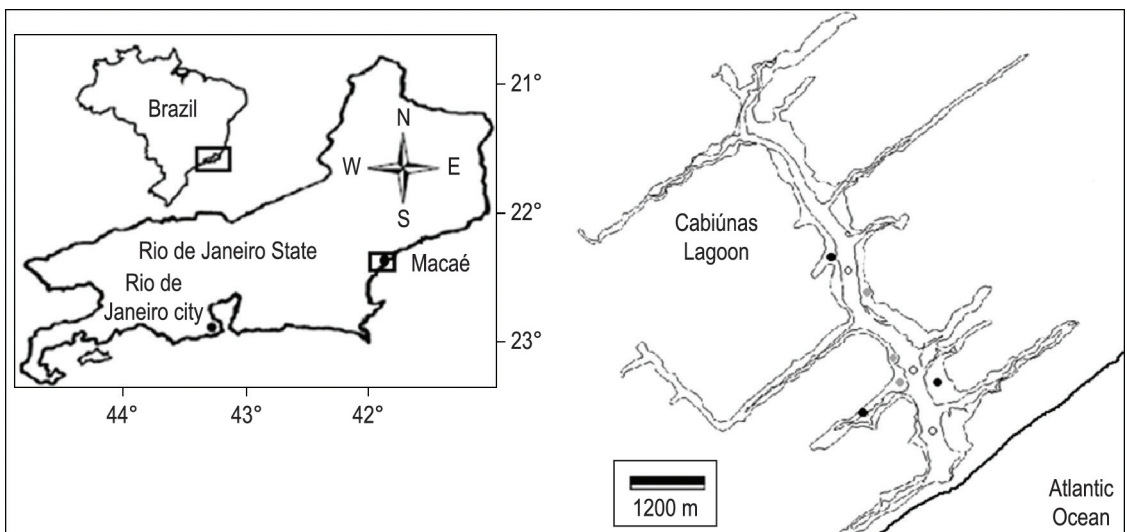


Figure 1. Location of sampling sites in the Cabiúnas lagoon. (open circles – Limnetic region; black circles – *T. domingensis*; gray circles – *E. azurea*).

2.2. Samplings

Field samplings were performed throughout the summer season, between the years of 2009 and 2010. Spatial variability was evaluated by sampling CO₂ flux in three sites in each compartment (stands of *Typha domingensis*, *Eichhornia azurea* and limnetic region) (Figure 1). In each site, samplings were performed between 10 a.m. and 3 p.m. for five days in the macrophyte stands and for three days in the limnetic region.

2.2.1. CO₂ flux

CO₂ flux was measured by single-component static closed chambers, which were chosen because they are low-cost and require simple operation mechanisms and no electric power in the field or during on-line measurement. In addition, these chambers do not require large experimental areas and are portable, allowing process studies and experiments with many treatments (Denmead, 2008). A single-component chamber was deployed in a single step, so that it completely enclosed a volume of air once sealed to the water or soil surface. Such chambers do not allow air circulation between the chamber and the sensor; periodic air samples were taken from the headspace using a gas syringe and the gas concentrations were later determined in the lab. Although higher concentration changes are easier to detect, it is very difficult to deploy these chambers correctly. If any physical disturbance is made to the measurement site during chamber placement, it may alter the observed exchange rate (Denmead, 2008; Livingston and Hutchinson, 1995). As was proposed by Livingston and Hutchinson (1995), such problems were minimized

by selecting the best chamber size and time and avoiding disturbances to the water surface and the macrophyte stands during deployment.

Aiming to evaluate the contribution of the limnetic region to CO₂ balance, CO₂ concentrations were sampled in transparent acrylic chambers (0.25 m² × 0.3 m; Figure 2) at intervals that ranged from 5 min to 15 min. The contribution of macrophyte stands was evaluated by comparing measurements taken from sites with or without macrophytes in the littoral region. CO₂ flux through water surface on macrophyte stands was determined using a similar chamber (Figure 2) and, at the same time, CO₂ flux was described for the limnetic sites. In the presence of *E. azurea*, a similar chamber or a plastic transparent chamber (0.25 m² × 0.7 m; Vulcan plastic – 0.6 mm; Figure 2) was used to determine CO₂ concentrations. For *T. domingensis*, we evaluated CO₂ flux using plastic transparent chambers (0.07 m² × 2 m; Vulcan plastic – 0.6 mm, Figure 2). In the presence of macrophytes, CO₂ concentrations in the chamber were sampled at intervals between 3 and 9 min. Periodic air samples were taken from the head-space with a 3 mL gas syringe sealed with a stop-cock. CO₂ concentrations in the syringes were determined in the lab by gas chromatography during a 48-hour time period on a gas chromatograph (Shimadzu GC-2010) equipped with a flame ionization detector (FID). CO₂ was catalytically converted to CH₄ prior to the analysis by flushing the gas with hydrogen through a nickel powder filled methanizer.

2.2.2. Physic-chemical parameters

At each site, we determined depth, salinity (YSI-30) and oxygen (YSI-95 sonde) concentration in

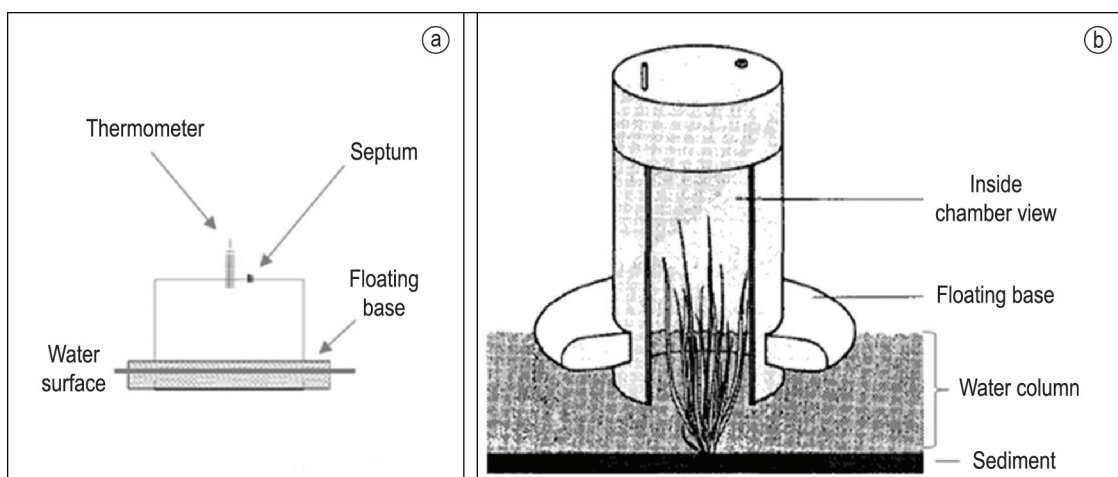


Figure 2. Schematic figure representing chambers for sampling CO₂ fluxes in the absence (a) and presence (b) of aquatic macrophytes. (Adapted from Livingston and Hutchinson, 1995).

the water column; air temperature and wind speed (anemometer Kestrel-2000) in the atmosphere; and photosynthetically active radiation (PAR) with a radiometer (LI-COR-1000) in macrophyte stands. By the end of the sampling process, macrophyte leaf number inside the chamber was determined and leaf stand density was assessed as a function of chamber area.

2.3. Flux determination

Once closed chambers have no or a very small amount of air in the headspace, gas concentration continually increases (Denmead, 2008). Therefore, increasing rates are monitored and a linear model can be used to estimate gas flux. The gas flux density at the surface F_g ($\text{mg}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) is calculated from:

$$F_g = (V/A)dp_g/dt \quad \text{Equation 1}$$

where V (cm^3) is the volume of the headspace, A (m^2) is the surface area covered by the chamber, dp_g ($\text{mg}\cdot\text{cm}^{-3}$) is the gas concentration in the air entering or leaving the chamber and t (s) is the time. Flux was integrated by Linear Regression models. Only CO_2 fluxes rating $R^2 > 0.5$ were considered in the present study. The flux from chambers with macrophytes inside was subtracted from chambers without macrophytes in each stand to estimate CO_2 fluxes from macrophyte tissues.

2.4. Macrophytes cover

The area and the proportion of macrophyte cover of Cabiúnas lagoon were estimated by GIS analysis (software ArcGIS 9.3). A satellite image was taken in 01/23/2010 from CBERS (INPE). The proportion of *T. domingensis* and *E. azurea* stands in the Cabiúnas lagoon was estimated on site by profile and belt transect methods (Jensen, 1977) based on the lagoon's area and perimeter. The Cabiúnas lagoon covers 0.75 Km^2 area and has a 21.5 Km perimeter, so 1 m-large transects (40) were evaluated (Figure 3). Data extrapolation was based on the spatial representation from each micro-site evaluated in the ecosystem (Schimel and Potter, 1995).

2.5. Data analysis

Differences in flux patterns from chambers without macrophytes were statistically analyzed using a parametric ANOVA on a factorial-design, being CO_2 fluxes sampled each day on the three sites the dependent variable and compartments the categorical ones (significance level – $p = 0.05$). In chambers with macrophytes, unpaired T-tests were used (p) - 0.05 for comparisons between CO_2 fluxes

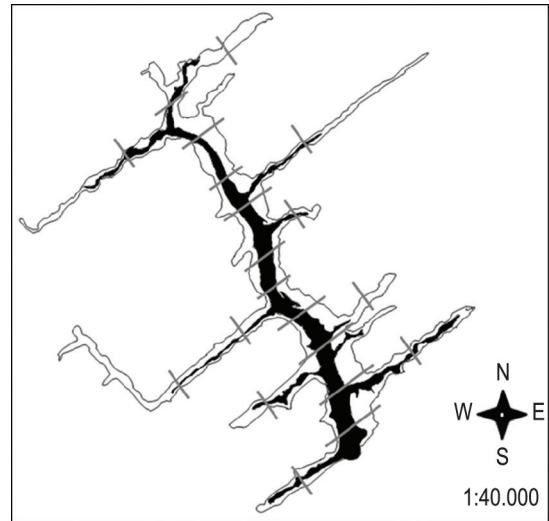


Figure 3. Profiles sampled in the Cabiúnas lagoon. Each profile consisted of 2 transects, thus 40 total transects were performed. (White – Aquatic macrophytes cover; black – lagoon water; grey bars - profiles).

from *T. domingensis* and *E. azurea* compartments. Paired T-tests were used to compare fluxes from chambers with and without macrophytes in *T. domingensis* and *E. azurea* stands ($p < 0.05$). All analyses were performed using the software Statistica 8.0, and graphs were made in GraphPad Prism 5.

The models that best described the relationship between CO_2 flux and physical/chemical features were selected by Akaike's Information Criterion (AICc). Akaike's weight for each model (w_i) provides evidence to show which model best explains the data. Model plausibility decreases with increasing ΔAICc , and therefore, this measure offers empirical support for a given model (Burnham and Anderson, 2002). A ΔAICc difference of 3, in relation to the best model, was accepted as sufficient to explain the other models. Analyses were performed using the software SAM, version 4.0 (Rangel et al., 2010).

3. Results

3.1. CO_2 fluxes from water surface and macrophytes tissues

CO_2 effluxes from the water surface were similar among the three sampling sites (Figure 4; ANOVA $F = 2.72$; $p = 0.08$). Mean fluxes at the limnetic region were $4.82 \pm 2.76 \text{ mg CO}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ (ranging from 2.38 up to $10.21 \text{ mg CO}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) (Figure 4). In macrophyte stands, CO_2 effluxes were $4.16 \pm 4.83 \text{ mg CO}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ (ranging from -7.39 up to $13.90 \text{ mg CO}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) and $7.49 \pm 4.00 \text{ mg CO}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ (ranging from 3.21 up to 17.56

mgCO₂.m⁻².h⁻¹) in *T. domingensis* and *E. azurea* stands, respectively (Figure 4).

More than 90% of CO₂ flux through macrophytes were negative. CO₂ influxes were higher in *T. domingensis* than in *E. azurea* stands ($t = 2.126$; $p = 0.047$). Mean fluxes in *T. domingensis* stands were -229.1 ± 320.9 mg CO₂.m⁻².h⁻¹ (ranging from -610.1 up to 630.4 mg CO₂.m⁻².h⁻¹) and in *E. azurea* stands were -43.8 ± 39.5 mg CO₂.m⁻².h⁻¹ (ranging from -126.7 up to 9.1 mgCO₂.m⁻².h⁻¹) (Figure 5).

Flux from macrophyte stands show that CO₂ influx by aquatic macrophytes was higher than CO₂ efflux from the water surface (t -Test $t = -4.71$; $p < 0.001$ at *T. domingensis* stands; t -Test $t = -53.16$; $p < 0.001$ at *E. azurea* stands).

3.2. Factors driving CO₂ fluxes

Physical-chemical measured parameters are presented in Table 1. Salinity was the same (0.3‰) at all sampling sites, and thus, these data are not shown in Table 1 and were not considered by the model selection analysis.

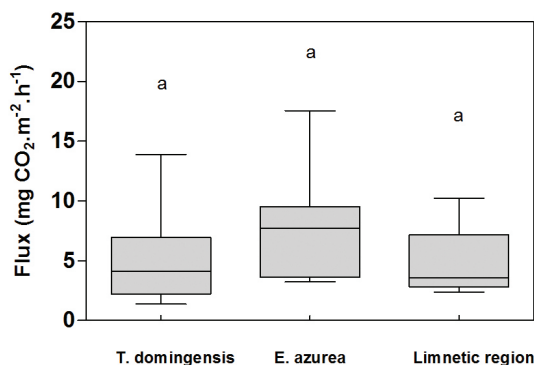


Figure 4. CO₂ efflux through the water surface at stands of *T. domingensis* and *E. azurea* and the limnetic region of the Cabiúnas Lagoon. The boxes represent the 25th to the 75th percentile and the lines represent the data range and the central lines are the averages. Similar letters represent non-significant differences among treatments.

According to Akaike's Information Criterion (AICc), the models that best fit the data distribution for CO₂ diffusion through the water surface included O₂ saturation near the water surface, air temperature, depth and wind speed (Table 2). For CO₂ flux through macrophytes, the best models included leaf density, wind speed, PAR, air temperature and depth (Table 3). All physical-chemical features were selected by AICc for flux in the limnetic and the littoral regions.

3.3. Macrophyte cover and CO₂ balance in the Cabiúnas Lagoon

The analysis from satellite images showed that 60.5% of the Cabiúnas lagoon area was covered by aquatic macrophytes. In total, 1591 m² of macrophyte stands were evaluated in 40 transects. *Typha domingensis* and *Eichhornia azurea* covered 44.7% and 14.4% of the total plant area, respectively, which corresponds to 0.20 Km² and 0.07 Km² of the Cabiúnas lagoon's area.

The limnetic region tends to emit CO₂ at a low rate (1.43 mgCO₂.m⁻².h⁻¹), but patterns in macrophyte stands are the opposite. The CO₂

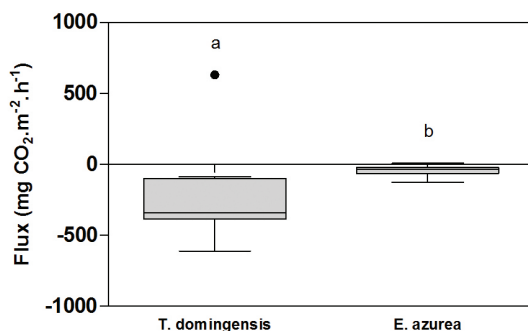


Figure 5. CO₂ influx from macrophytes at stands of *T. domingensis* and *E. azurea* in the Cabiúnas Lagoon. The boxes represent the 25th to the 75th percentiles, lines represent the data range and the central lines are the averages. Black balls represent outliers. Different letters represent significant differences between treatments.

Table 1. Physical-chemical parameters that represent the main factors driving water-atmosphere CO₂ flux in the Cabiúnas lagoon (mean and standard deviation).

	Sites		
	Open water	<i>T. domingensis</i>	<i>E. azurea</i>
Wind speed (m.s ⁻¹)	5.5±2.2	4.0±1.4	5.0±1.0
Air Temperature (°C)	28.3±1.4	31.7±3.8	29.6±2.9
PAR (μmol fotons.m ⁻² .s ⁻¹)	-	1203.8±491.6	782.0±384.5
Dissolved oxygen (%)	54.2±4.6	52.1±16.7	41.7±16.1
Depth (m)	2.70±0.65	1.70±0.20	2.20±0.25
Leaf density (Leaf.m ⁻²)	-	141.5±41.7	47.5±14.7

Table 2. AIC selected models to explain CO₂ diffusion through the Cabiúnas water surface.

Model	Code	AIC _c	ΔAIC _c	Wi	Coefficient
[O ₂] surface	1	255.98	0	0.223	+
Air Temperature	2	257.10	1.124	0.127	+
Depth	3	257.33	1.354	0.113	+
[O ₂] surface, Depth	4	257.47	1.493	0.106	+ +
[O ₂] surface, Wind speed	5	258.03	2.058	0.080	+ +
Air Temperature, [O ₂] surface	6	258.34	2.361	0.068	+ +
Air Temperature, Depth	7	258.42	2.443	0.066	+ +
Air Temperature, Wind speed	8	259.07	3.098	0.047	+ +

Table 3. AIC selected models to explain CO₂ flux through aquatic macrophytes in the Cabiúnas lagoon.

Model	Code	AIC _c	ΔAIC _c	Wi	Coefficient
Leaf density	1	587.68	0	0.259	-
Wind speed, Leaf density	2	589.15	1.465	0.125	+ -
PAR, Leaf density	3	589.21	1.531	0.121	+ -
Air Temperature Leaf density	4	589.74	2.06	0.093	+ -
Depth, Leaf density	5	590.05	2.368	0.079	- -
PAR, Wind speed, Leaf density	6	590.97	3.291	0.050	+ + -

balance in *T. domingensis* and *E. azurea* stands showed an incorporation rate of 45.6 and 2.37 mg CO₂.m⁻².h⁻¹, respectively. Such macrophytes cover less than a third of the lagoon but incorporate an estimated 92.3% (*T. domingensis*) and 4.8% (*E. azurea*) of the total CO₂. The limnetic region corresponds to 40% of the free water surface and emits only 2.8% of the CO₂ estimated in this study. As a result, we estimate that 75% of Cabiúnas lagoon's area incorporates 46.6 mg CO₂.m⁻².h⁻¹.

4. Discussion

CO₂ emission has been one of the most important topics in research on the C cycle in lakes. Lakes are large aquatic ecosystems that have been seen as net heterotrophic systems, acting as large sources of greenhouse gases released into the atmosphere (Cole et al., 1994; Sobek et al., 2005; Marotta et al., 2009). However, previous studies focused on the balance among processes that produce and consume CO₂ in the water column (i.e., planktonic respiration and photosynthesis) and neglected littoral zones. The presence of aquatic

macrophytes in lakes represents a great potential for CO₂ absorption. Such potential was the central question addressed by the present investigation.

We observed that lake areas with no plant cover in Cabiúnas lagoon, such as the limnetic region and some zones within aquatic macrophyte stands, showed positive diffusive CO₂ flux (effluxes). Indeed, Cabiúnas is a humic lagoon, and thus, its water column is CO₂ supersaturated, acting as a CO₂ source to the atmosphere (Marotta et al., 2010). In addition, CO₂ diffusive efflux through the water surface, in sites with and without macrophytes, suggests that such plants have a small or no effect in CO₂ saturation in the water column as well as no effect on CO₂ flux at the water-atmosphere interface. However, some evidences found sites nearer to emergent aquatic macrophyte stands supported higher *p*CO₂ than open-water sites in the Cabiúnas lagoon (Marotta et al., 2010). Their results are consistent with the reported role played by aquatic macrophytes on enhancing CO₂ inputs to lake water columns (Caraco et al., 2006) and, subsequently, to water saturation (Cole et al., 1994) and higher CO₂ emission from the water into

the atmosphere. The lack of such positive effect of aquatic macrophytes and CO₂ effluxes observed in the present study, may be explained by other physical factors affecting this process, such as the reduced influence of wind in these sites. Wind speed was positively related to CO₂ flux and was included in models selected by the AICc. However, all of the physical-chemical features were selected by AICc for diffusive flux, suggesting that there is no one major parameter influencing CO₂ diffusive flow patterns. In addition, it is important to highlight that productivity and respiration (decomposition) may be not coupled in aquatic ecosystems; they present temporal disconnections that can result in periods of different CO₂ diffusive flow patterns (Guariento et al., 2009). Therefore the time scale that is chosen for CO₂ diffusive measurements may favor specific patterns than others, which can explain the divergence among studies that used non-standardized methodologies.

There was a net CO₂ influx in sites colonized by *Typha domingensis* and *Eichhornia azurea* in Cabiúnas lagoon. This influx resulted in an expressive C incorporation into macrophytes tissues and CO₂ assimilated by macrophytes attenuated that released by Cabiúnas lagoon water surface, resulting on a net CO₂ input to the ecosystem. Indeed, most coastal ecosystems dominated by macrophytes are highly productive and overall autotrophic (Duarte and Cebrian, 1996). Littoral zone production has often been found to dominate total lake production, especially in shallow lakes where a large part of the lake's surface area lies within the littoral zone (Loeb et al., 1983). Once flux rates were measured during daylight, carbon fixation by photosynthesis were the dominant process in macrophyte stands, exceeding total respiration. The same trend has been observed by other researchers in wetland ecosystems (Bolpagni et al. 2007; Zhou et al., 2009).

In this study, the models that best described CO₂ influx through macrophytes included leaf density parameters in an antagonistic relation to CO₂ flux. The fact that CO₂ incorporation and leaf density are higher in *T. domingensis* than *E. azurea* suggests that species have a larger variation in gross community production. Considering both evaluated species and the area they cover, CO₂ incorporation by *T. domingensis* stands was much higher than *E. azurea* stands at Cabiúnas lagoon. Differences on the gross community productivity, measured by CO₂ assimilation, have also been shown on a temperate coastal lagoon, comparing *Spartina maritima* stands to *Zostera noltii* ones (Silva et al., 2005). Since

macrophyte assemblages tend to have a spatial segregation (Boschilia et al., 2008), the amount of CO₂ assimilated may differs among the littoral zone of lakes due to the change in species cover. Thus, C cycling in lakes' littoral zones may be strongly determined by species identity when estimating C balance in aquatic ecosystems.

Studies on the contribution of *T. domingensis* to C cycling in the sediment and the water column in the Cabiúnas lagoon are long-lasting. In research on aquatic macrophyte decomposition and detritus from terrestrial vegetation in the lagoon, *Typha domingensis* detritus exhibited the slowest decomposition rate (Farjalla, et al., 1999). Higher C concentration in sediment colonized by macrophytes indicated that such species give a large contribution to organic matter composition in this compartment (Marinho et al. 2010). Since *T. domingensis* covers almost 45% of the area occupied by aquatic plants at the Cabiúnas lagoon, it can be considered one of the main sources of slowly mineralized organic matter that is accumulated in this environment. Research on biodiversity and ecosystem functioning has emerged as a major sub-discipline in the field of ecology and has shown that the magnitude of individual species' effects on ecosystem functioning is variable. Then, species-rich communities may have more influence on ecosystem functioning than species-poor communities, on average, because they are more likely to contain species that have large effects on ecosystem functioning (Huston, 1997). Therefore, especially in macrophyte species rich lakes, our results suggest that it is important considering macrophyte species composition to understand the role of spatial variation on C balance estimation.

Beyond CO₂ fluxes, the importance of aquatic macrophytes to C balance in coastal lagoons is also related to the dynamic of some other compounds, such as methane (Fonseca et al., 2004, Petruzzella et al., 2013). Aquatic plant roots influence the activity of microorganisms through organic matter production and oxygen transportation to the rhizosphere (Garnet et al. 2005). On the other hand, methane found in the sediment can be transported to the atmosphere across the macrophytes' aerenchyma tissues (Laanbroek, 2010), reducing gas consumption and carbon accumulation in the sediment. Although the amount of methane emitted into the atmosphere is just a relatively small proportion of the total C accumulated in the sediment, it can be significant in terms of global warming due to

methane's potential to absorb infrared radiation in the atmosphere (IPCC, 2007). If considered the contribution of *Phragmites australis* to C balance coupled with different physical features of the two gases (CO₂ and CH₄), wetlands can increase the greenhouse effect on a short time scale basis because of methane emission (Brix et al., 2001). However, such ecosystems also work as a greenhouse gas sink, forcing the gases to attenuate it if they are evaluated over longer time scales. Therefore, despite our results on CO₂ incorporation, the contribution of aquatic macrophytes, mainly *Typha domingensis*, to greenhouse gas emission in the Cabiúnas lagoon still needs to be estimated. Because methane exerts a significant effect on global heat balance in the atmosphere (Mosier, 1998), the balance between CO₂ incorporation and methane emission by *Typha domingensis* will estimate the true role played by this macrophyte on the C cycle in the Cabiúnas lagoon.

Despite the lack of precise estimates of the general role of aquatic macrophytes in the C cycle in Cabiúnas lagoon, our study provides valuable information about the role of macrophytes in the CO₂ dynamics in this lagoon. Our findings are particularly important for the functioning of wetlands and shallow lakes, where macrophytes colonization, diversity and lake cover is generally high and the littoral–pelagic connectivity assume greater importance for subsidizing ecosystem-level process such as aquatic metabolism (Scheffer 1998; Schindler and Scheuerell, 2002). In these systems, further investigations should focus on evaluating the contribution of different species to lake metabolism and C cycle as well as the long term response of macrophyte storage and decomposition in the ecosystem.

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