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Key Points:

- CO₂ concentrations in near-surface waters within flooded Amazon forests ranged from 19 to 329 μM and CO₂ fluxes from -0.8 to $55 \text{ mmol m}^{-2} \text{ hr}^{-1}$
- Daytime CO₂ fluxes were higher at a wind-protected site, while night-time fluxes were often higher at a wind-exposed site
- On an areal basis, CO₂ fluxes from flooded forests during high water levels are the major contributor among aquatic habitats

Supporting Information:

- Supporting Information S1

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Carbon Dioxide Fluxes to the Atmosphere From Waters Within Flooded Forests in the Amazon Basin

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Abstract Inundated tropical forests are underrepresented in analyses of the global carbon cycle and constitute 80% of the surface area of aquatic environments in the lowland Amazon basin. Diel variations in CO₂ concentrations and exchanges with the atmosphere were investigated from August 2014 to September 2016 in two flooded forests sites with different wind exposure within the central Amazon floodplain (3°23'S, 60°18'W). CO₂ profiles and estimates of air–water gas exchange were combined with ancillary environmental measurements. Surface CO₂ concentrations ranged from 19 to 329 μM , CO₂ fluxes ranged from -0.8 to $55 \text{ mmol m}^{-2} \text{ hr}^{-1}$ and gas transfer velocities ranged from 0.2 to 17 cm hr^{-1} . CO₂ concentrations and fluxes were highest during the high water period. CO₂ fluxes were three times higher at a site with more wind exposure (WE) compared to one with less exposure (WP). Emissions were higher at the WP site during the day, whereas they were higher at night at the WE site due to vertical mixing. CO₂ concentrations and fluxes were lower at the WP site following an extended period of exceptionally low water. The CO₂ flux from the water in the flooded forest was about half of the net primary production of the forest estimated from the literature. Mean daily fluxes measured in our study ($182 \pm 247 \text{ mmol m}^{-2} \text{ d}^{-1}$) are higher than or similar to the few other measurements in waters within tropical and subtropical flooded forests and highlight the importance of flooded forests in carbon budgets.

Plain Language Summary Aquatic habitats in the lowland Amazon emit large quantities of carbon dioxide (CO₂). However, information on CO₂ fluxes from seasonally flooded forests that constitute 80% of the surface area of aquatic environments in the lowland Amazon basin is sparse. We provide the first multi-year measurements of CO₂ exchanges within flooded forests of the central Amazon basin. Our approach combines measurement of dissolved CO₂ concentrations and fluxes between the water and atmosphere and ecological data. Although the rates of CO₂ emission by flooded forests are lower than other aquatic habitats, such as open waters in rivers and lakes, the combination of high CO₂ concentrations and a large area results in an appreciable regional outgassing of carbon dioxide from flooded forests. These fluxes can represent about half of the net primary production of flooded forests in the central Amazon basin.

1. Introduction

Recent syntheses of carbon processing and evasion to the atmosphere from inland aquatic ecosystems have revealed the disproportionately large contribution, relative to their area, that these ecosystems make to carbon cycling and the importance of outgassing of carbon dioxide (Cole et al., 2007; Lehner & Döll, 2004; Raymond et al., 2013). Tropical freshwater systems are underrepresented in these analyses, and seasonally, inundated forests are seldom considered. Within the lowland Amazon basin, seasonally inundated and riparian forests cover approximately 750,000 km^2 , 15% of the whole lowland area, and are important to the ecology and biogeochemistry of the region (Junk et al., 2010; Melack & Hess, 2010). Floodplain forests occur in an aquatic terrestrial transition zone (ATTZ; Junk et al., 1989) and are inundated for varying portions of the year depending on water level and local topography (Wittmann et al., 2010). Inundated forests and other floodplain habitats add organic carbon and dissolved CO₂ to floodplains and rivers (Melack & Engle, 2009; Melack & Forsberg, 2001; Worbes, 1997) and contribute to evasion of CO₂ and methane from

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these aquatic environments (Abril et al., 2014; Melack, 2016; Melack et al., 2004; Pangala et al., 2017; Richey et al., 2002). However, almost all studies of CO₂ outgassing from Amazon floodplains have been restricted to open water areas.

CO₂ exchanges with the atmosphere are determined by the gradient of water–air CO₂ concentrations and by the gas transfer velocity (k), a function of turbulence at the air–water interface (MacIntyre et al., 1995; Zappa et al., 2007). Most computations of carbon fluxes from lakes and wetlands use simple wind-based equations of k , though other mechanisms are recognized as important in tropical, temperate, and arctic lakes (MacIntyre et al., 2002; MacIntyre et al., 2018; MacIntyre & Melack, 1995; Tedford et al., 2014), as well as wetlands (Poindexter et al., 2016). Vegetated aquatic habitats, such as flooded forests, are likely to experience lower wind speeds than open water areas. However, diel variations in cooling or heating of surface waters and associated horizontal water motions and convective mixing can enhance gas exchange even at low wind speeds (MacIntyre et al., 2019). Direct measurements of k , water–air CO₂ concentration gradients, and meteorological parameters in flooded forests are needed to better understand the mechanisms associated with CO₂ outgassing from these aquatic habitats and to evaluate their role in the carbon cycle.

The first regional estimate of CO₂ outgassing for the aquatic habitats of the Amazon basin (Richey et al., 2002) reported CO₂ outgassing of $830 \pm 240 \text{ Mg C} \cdot \text{km}^{-2} \text{ yr}^{-1}$. Subsequent measurements conducted in lakes (Polisenaere et al., 2013; Rudorff et al., 2011), reservoirs (Kemenes et al., 2011), and rivers (Alin et al., 2011; de Rasera et al., 2013; Sawakuchi et al., 2017) reported higher k values compared to the values used by Richey et al. (2002). Although seasonally flooded forests can cover large areas, data on k and CO₂ concentrations and fluxes in these habitats are lacking and likely are different from the conditions in the lakes, reservoirs, and rivers.

Our study contributes to understanding of Amazon floodplains and regional carbon cycling. We provide new information on CO₂ dynamics in inundated forests, the largest aquatic habitat in the Amazon basin, but the one least studied. We report CO₂ concentrations, evasion rates, and gas transfer velocities measured in flooded forests fringing a floodplain lake along the Solimões River as function of seasonal changes in water depth and day to night differences over the course of two distinct hydrological years. Contrasting exposure to wind is considered in our analysis, and we test the following hypotheses: (1) The proximity and the extent of open water areas close to flooded forest sites will lead to different CO₂ fluxes in the forests. (2) Wind-protected forests will have lower k values and consequently lower CO₂ fluxes than wind-exposed sites. (3) Flooded forests have high rates of CO₂ evasion to the atmosphere and make a large contribution to regional CO₂ evasion in the Amazon basin.

2. Methods

2.1. Site Description and Sampling

Measurements over 2 years were made in two contrasting flooded forest sites in Lake Janauacá (3°23'S, 60°18'W; altitude 32 m), located on the southern side of the Solimões River in the central Amazon basin (Figure 1). The sites differed in wind exposure and fetch of adjacent open water areas and are called wind-exposed flooded forest (WE; 3°23'19.0"S, 60°15'14.8"W) and wind-protected flooded forest (WP; 3°24'20.6"S, 60°14'48.8"W). The WP site is in an embayment with a fetch of 50 to 100 m for typical wind directions. The WE site is located on the edge of the main lake and had a fetch varying from 1 to 4 km depending on wind direction and water level.

The forests investigated are influenced by sediment and nutrient rich water from the Solimões River and are called *várzea* forests (Wittmann et al., 2002). Trees on these floodplains respond phenologically, morphologically, and physiologically to periodic flooding that varies as a function of the water level of the Solimões River and the topography of the ATTZ (Parolin et al., 2010; Worbes, 1997). Phenological behavior is largely associated with the time and extent of inundation, and evergreen, semideciduous, and deciduous species shed their leaves at different times (Parolin et al., 2010). *Piranhea trifoliata* and *Vitex cymosa* are common tree species (Worbes et al., 1992). The Janauacá floodplain and nearby systems have been the focus of prior studies of hydrology and limnology (Bonnet et al., 2017; Melack et al., 2009; Melack & Forsberg, 2001).

Measurements of carbon dioxide partial pressure ($p\text{CO}_2$) and CO₂ emissions were made when the sites were flooded and accessible at multiple times of the day and night. Measurements were made on 12 occasions

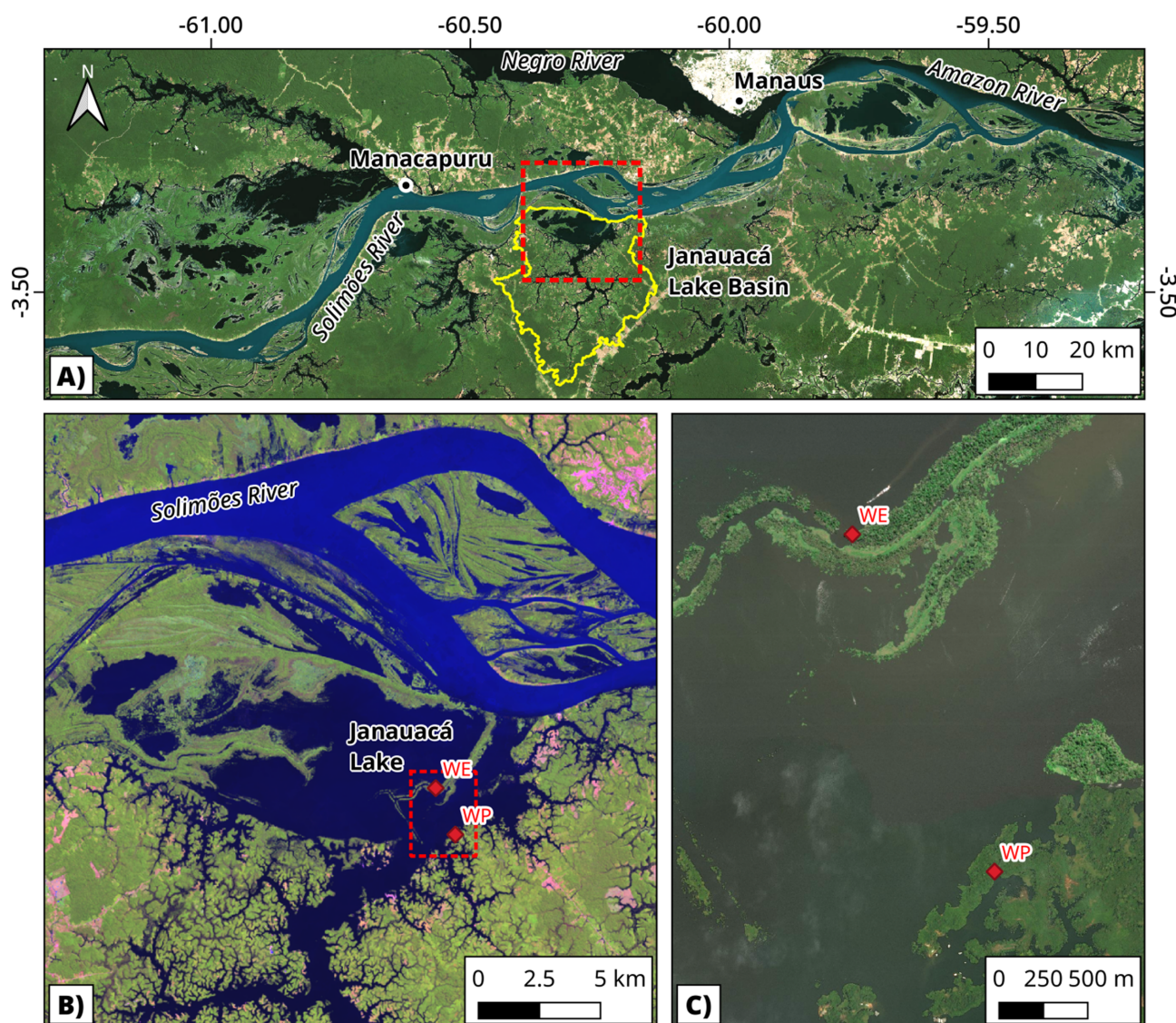


Figure 1. (a) General location of the study site showing the watershed (yellow line; Background: ESRI World Imagery). (b) Composite high-water Landsat 8 image showing the upper Janauacá floodplain (red dashed). (c) Location of the sampled flooded forest sites: wind-exposed site (WE) and wind-protected site (WP). Red dashed lines indicate the boundaries of the following figure panel. Janauacá lake basin delimited by Pinel et al. (2015).

between August 2014 and September 2016, representing different hydrological phases. The following periods were sampled: August 2014 (falling water—FW), February to April 2015 (rising water—RW), May to July 2015 (high water—HW), August 2015 (FW), September 2015 (FW), July 2016 (HW), and August and September 2016 (FW). The WP site was sampled in all campaigns, while the WE site only in 2015 (Figure S1 in the supporting information).

2.2. Analytical Methods

$p\text{CO}_2$ was measured with an off-axis integrated cavity output spectrometer (Ultraportable Greenhouse Gas Analyzer, Los Gatos Research) connected to a marble-type equilibrator (Frankignoulle et al., 2001), through which water from different depths was pumped (3 L min^{-1}). CO_2 fluxes across the air–water interface were measured using floating chambers connected in a closed loop to the Ultraportable Greenhouse Gas Analyzer. All measurements were made in replicate as ~ 10 -min deployments from a moored boat. The chambers had an internal volume of 15 L and an internal area of 0.11 m^2 . Fluxes were calculated from the slope of partial pressure versus time, which was linear with r^2 greater than 0.9. The detection limit of our fluxes measurements was calculated as $0.22 \text{ mmol m}^{-2} \text{ hr}^{-1}$ of CO_2 . Further details of the

equilibrator setup and gas analyzer accuracy are given in Amaral et al. (2018) and for the chamber design in Barbosa et al. (2016).

We estimated gas transfer velocity (k) from the formulation $F = k[\Delta\text{CO}_2]$ using our measurements of CO_2 fluxes (F) and the difference between observed and equilibrium gas concentrations (ΔCO_2) derived from the $p\text{CO}_2$ measurements in water and air and using Henry's constant. To estimate the gas concentrations in water and air, we first corrected the dry air in the instrument to wet air using the water vapor computed from temperature measured at lake surface (Weiss & Price, 1980), and then used the Henry's constant for CO_2 from Wiesenburg and Guinasso (1979) to calculate concentration. Estimated k values were normalized to 20 °C (k_{600}) for which 600 is the Schmidt number for CO_2 at 20 °C and Sc at other temperatures were obtained from Wanninkhof (1992).

Near-surface pH (Orion Star, Thermo Scientific; precision of 0.1, calibrated with 4.0, and 7.0 standards), maximum depth measured with a weighted graduated line, and depth profiles of conductivity and temperature measured with a profiler (Castway, Sontek Inst. Co) at 0.3 m intervals were obtained during each sampling period. Time series measurements of temperature and dissolved oxygen (DO) were obtained at each site using thermistors with 0.002 °C accuracy (RBRsolo) recording every 0.5 s, and with optical DO sensors (PME MiniDOT loggers) recording every 10 min (accuracy of 5% of measurement or 0.3 mg L⁻¹, whichever is larger, and resolution of 0.01 mg L⁻¹). Wind speed and direction sensors (Onset, Inc.) were deployed at a height of 2 m on a floating buoy at open water sites close to flooded forest sites. Average wind speeds were calculated for the hour before the flux measurements.

Samples from ~0.3 m for chlorophyll (Chl-*a*), dissolved organic carbon (DOC), total suspended solids (TSS), total nitrogen (TN), and total phosphorus (TP) analyses were collected once on each campaign at both stations. Chl-*a* samples were filtered through glass fiber GF/F filters (Whatman) and kept frozen in the dark until analysis. Chl-*a* was determined spectrophotometrically, following filter maceration and extraction in 90% acetone, using the trichromatic equations of Strickland and Parsons (1972). TSS was determined by weighing particulates collected on pre-weighed Millipore HA filters (0.45 μm pore size), following the method of Kasper et al. (2018). DOC samples were filtered through pre-combusted (450–500 °C for 1 hr) glass fiber GF/F filters (Whatman), collected in pre-cleaned (10% HCl wash, deionized water rinse) and pre-combusted (450–500 °C for 1 hr) borosilicate vials, and then stored at 4 °C until analysis. DOC was determined using a total organic carbon analyzer (TOC-V Shimadzu). TN and TP were determined by simultaneous analysis on unfiltered samples after persulfate digestion (Valderrama, 1981) followed by nitrate and phosphorus assays (Strickland & Parsons, 1972).

We estimated flooded forest area for the northern portion of Janauacá for each sampling date using an image classification method to discriminate floodable forest habitats and other land covers and a digital elevation model derived for the lake (Pinel et al., 2015). Forest vegetation (including trees and shrubs) was classified using all bands of a Landsat 8 OLI image acquired in April 2016, when all floodable shrubs and trees were emergent. We used eCognition software to perform multiresolution image segmentation, delineating homogeneous land cover units within the image. We then developed classification rules to discriminate forest and shrub areas based on the Normalized Difference Vegetation Index and the Normalized Difference Water Index (Gao, 1996). We used the digital elevation model and daily observations of water surface elevation, made at a differential GPS calibrated gauging station on the lake (Pinel et al., 2015), to estimate inundated area for each sampling occasion. Finally, we used the classified image together with the inundation maps to estimate the total area of flooded forest for each sampling period.

To account for the influence of forests with different wind exposure on CO_2 fluxes, we separated the flooded forest into two categories: (1) sheltered flooded forest (WP), representative of flooded forests at the WP site, and (2) WE, similar to that found at the WE site. To define the WE forest area, we delimited the perimeter of the largest open water area in the lake and then selected a 100 m band of forest immediately adjacent to this region. All remaining flooded forest was defined as WP. All analyses were done with ArcGIS version 11.0 (ESRI, Inc.).

To combine measurements of fluxes and estimates inundated forest areas to calculate annual fluxes (F , Gg C yr⁻¹) from the flooded forests in the northern region of Janauacá, an expression similar to that in Melack et al. (2004) was used:

$$F = \sum_{j=1}^2 \sum_{i=1}^8 (f_{ij} \cdot A_{ij} \cdot t),$$

f is the mean daily flux of CO₂ for each month and site (g C·m⁻² d⁻¹), A is flooded forest area for each month (km²), t is the number of days per month, i is the index for each month (from February to September), and j is the index for each site (WP and WE).

To estimate the uncertainty of the estimates, we conducted a Monte Carlo error analysis using the measurements obtained each month and for data lumped into RW, HW, and FW periods. To do so, we randomly resampled with repetition the measurements for each period to create 100 artificial data and computed the arithmetic mean (m) and standard deviation (std) of these data using the *bootstrap* function in Matlab. We then computed the maximum likelihood estimators as $MLE = \exp(m + std^2/2)$ and 95% confidence intervals (CI; Dixon, 1993).

2.3. Statistical Analyses

CO₂ concentration, k_{600} , and CO₂ fluxes were compared between WP and WE sites for only the first year as WE sites were not accessible in the second year. Tests for normality and homoscedasticity indicated that CO₂ concentrations were normally distributed, but k_{600} and CO₂ fluxes were not unless log transformed. Parametric tests were used in all comparisons, using log transformed data, as required. The student t test was used for comparisons between WP and WE sites. A one-way analysis of variance (ANOVA) followed by post hoc pair-wise t tests, with correction for multiple tests done by the Benjamin–Hochberg method, was used to compare hydrological periods. We separated measurements conducted over 24 hr into categories of day (6:00 a.m. to 6:00 p.m.) and night (6:00 p.m. to 6:00 a.m.) to evaluate the implications of sampling time for CO₂ fluxes, variability of k_{600} , and CO₂ concentrations. We compared day and night values using all data and data separated by site by paired t test.

To assess the potential influences of environmental variables on CO₂ concentrations measured in flooded forests with contrasting wind exposure, we applied a multimodel selection and averaging approach (Grueber et al., 2011) of linear mixed-effects models with maximum likelihood using the *lme4* package in R. The model was structured with CO₂ concentration as a response variable, site (WP and WE) as random factors, and the total area of flooded forest for each sampling period, surface temperature, TSS, DO, TN, TP, DOC, and Chl- a as fixed variables. We generated and evaluated the small-sample corrected Akaike information criterion (AICc), $\Delta AICc$, and AICc model weights (w_i) using the *dredge* function within the *MuMIn* package (Barton & Barton, 2018). The final model sets were simplified from all possible models by retaining only the top models within two units of $\Delta AICc$ of the “best” model. We calculated a daily geometric mean of CO₂ concentration for each site and sampling occasion and used these values in the models, as we made only one measurement in each campaign for some environmental predictors: Chl- a , TP, TN, DOC, and TSS. Before model selection, we first tested for outliers among explanatory variables (one exclusion was made). Second, we identified and excluded from the full model colinear predictors. For these steps, we use the outlierTest and vif function, respectively, both within the package car (Fox et al., 2012).

To estimate parameter coefficients in the final model set, we calculated conditional values using the mean of regression coefficients weighted by the AICc weight (w_i) from each model including that variable (Burnham & Anderson, 2002). Predictor relative importance or variable weights were calculated for each term in the models via the natural average method for the coefficients, that is, by summing the weights of models where each variable appears (Galipaud et al., 2014; Grueber et al., 2011). Using z tests, individual parameters in model-averaged sets were tested for statistical significance as the deviation of coefficients from zero. Parametric assumptions of linear models were verified using plots of residuals for normality and homoscedasticity. Statistical analyses and graphics were done with R Studio Version 1.1.456.

3. Results

3.1. CO₂ Concentrations and Fluxes

Surface CO₂ concentrations ranged from 19 to 329 μ M ($pCO_2 = 664$ to 11,006 μ atm); the overall geometric mean was 134 μ M, and the mean and standard deviation were 155 ± 71 μ M ($pCO_2 = 4,465$; $5,117 \pm 2,326$ μ atm; Table 1). One hundred seventy measurements of CO₂ flux were made at the two

Table 1Near-surface CO₂ Concentrations, Flux and Gas Transfer Velocities (k_{600}) Measured in Wind-exposed (WE) and Wind-protected (WP) Flooded Forests

Period	Month	CO ₂ (μM)		CO ₂ flux (mmol m ⁻² hr ⁻¹)		K_{600} (cm hr ⁻¹)	
		WP	WE	WP	WE	WP	WE
		Mean, SD (min/max, n)	Mean, SD (min/max, n)	Mean, SD (min/max, n)	Mean, SD (min/max, n)	Mean, SD (min/max, n)	Mean, SD (min/max, n)
Falling water	Aug 2014	158 ± 43 (112/216, 5)		2.8 ± 1.2 (0.9/4.6, 13)		1.5 ± 0.7 (0.4/2.6, 13)	
Rising water	Feb 2015	166 ± 53 (106/244, 5)	61 ± 37 (19/89, 3)	5.2 ± 3.2 (0.5/10.1, 13)	1.4 ± 1.8 (−0.8 ^a /3.9, 5)	2.5 ± 1.1 (0.3/4.2, 13)	4.1 ± 2.5 (1.7/8.0, 5)
	March 2015	90 ± 17 (81/110, 3)	100 ± 16 (87/118, 3)	3.4 ± 2.1 (1.6/5.7, 3)	3.2 ± 1.0 (2.3/4.3, 3)	3.3 ± 1.4 (1.8/4.5, 3)	2.9 ± 1.1 (1.8/4, 3)
	April 2015	156 ± 24 (137/184, 3)	237 ± 19 (226/259, 3)	8.5 ± 5.8 (3.4/14.6, 4)	17 ± 4.0 (11/22, 6)	5.3 ± 4.0 (1.8/9.5, 4)	6.4 ± 1.8 (3.7/8.3, 6)
	May 2015	202 ± 17 (186/221, 3)	236 ± 15 (219/246, 3)	7.7 ± 1.7 (5.4/10.5, 6)	36 ± 10 (18/48, 7)	3.2 ± 0.6 (2.3/4, 6)	12.8 ± 3.5 (6.8/16.8, 7)
High water	June 2015	217 ± 27 (189/243, 3)	227 ± 57 (177/289, 3)	6.9 ± 4.9 (4.4/16.7, 6)	30 ± 19 (13/55, 6)	2.6 ± 1.8 (1.6/6.2, 6)	10 ± 4.8 (4.9/16, 6)
	July 2015	190 ± 7 (182/196, 3)	187 ± 14 (174/202, 3)	4.6 ± 2.6 (1.7/9.1, 6)	30 ± 8.5 (13/33, 6)	2.1 ± 1.2 (0.8/4.2, 6)	9.7 ± 4.2 (5.6/15, 6)
	Aug 2015	265 ± 70 (177/329, 4)	180 ± 22 (163/213, 4)	5.4 ± 2.5 (2.7/9.7, 10)	16 ± 8.3 (8/31, 8)	1.6 ± 1.1 (0.7/4.3, 10)	7.4 ± 4.7 (2.9/16, 8)
Falling water	Sept 2015	157 ± 66 (83/244, 4)	172 ± 49 (123/250, 5)	2.6 ± 1.8 (1.4/7.3, 9)	6 ± 2.1 (3/10, 17)	2.1 ± 1.9 (0.7/6.9, 9)	3.3 ± 2.3 (1.3/8.3, 17)
	High water	111 ± 36 (80/164, 5)		3.6 ± 1.2 (2.1/5.4, 10)		3.1 ± 1.6 (1.8/5.9, 10)	
Falling water	Aug 2016	55 ± 13 (41/70, 5)		1.0 ± 0.3 (0.5/1.3, 11)		1.7 ± 0.3 (1.4/2.3, 11)	
	Sept 2016	94 ± 66 (24/203, 10)		1.7 ± 1.3 (0.1/4.8, 21)		1.9 ± 1.4 (0.2/6, 21)	

Note. SD is the standard deviation; min/max indicates the minimum and maximum values among the n measurements on each date.

^aThe ingassing value was measured when Chl-*a* concentrations were high (18 μg L⁻¹ in the flooded forest and 25 μg L⁻¹ in associated open water), suggesting that Chl-*a* enriched water was advected from the open water into the flooded forest site. One replicate measurement was negative, and one was positive; both had high r^2 (>0.95). When replicates were averaged, the value was slightly negative.

flooded forests sites, and fluxes ranged from −0.8 to 55 mmol m⁻² hr⁻¹ with an overall mean and standard deviation of 7.8 ± 10.1 mmol m⁻² hr⁻¹ (Table 1). Gas transfer velocities derived from these measurements ranged from 0.2 to 17 cm hr⁻¹ with an overall geometric mean value of 2.6 cm hr⁻¹ and mean and standard deviation of 3.8 ± 3.6 cm hr⁻¹ (Table 1). Mean CO₂ concentrations were similar at the two sites (WE, 175 ± 65 μM and WP, 178 ± 60 μM; Welch two sample *t* test, $t(58) = 0.2$, $p = 0.84$; Figure 2). CO₂ fluxes and k_{600} were greater at the WE site (16 ± 14 mmol m⁻² hr⁻¹ and 6.7 ± 4.6 cm hr⁻¹) compared to the WP site (5 ± 3 mmol m⁻² hr⁻¹ and 2.4 ± 1.7 cm hr⁻¹) based on Welch two sample *t* test ($t(82) = -5.4$, $p < 0.001$ and $t(112.2) = -7.9$, $p < 0.001$, respectively).

Surface CO₂ concentrations differed seasonally at the WE site based on one-way ANOVA ($F(2,24) = 4.9$, $p = 0.02$). Values were higher during high water (HW; 218 ± 36 μM, $n = 19$) relative to rising water (RW; 143 ± 89 μM, $n = 14$), but similar (pairwise *t* test, $p = 0.14$) to concentrations during FW (173 ± 39 μM, $n = 25$; Figure 2). Seasonal differences also occurred at the WP site ($F(4,48) = 9.9$, $p < 0.001$). In Year 1, the CO₂ concentrations measured at the WP site were higher during HW (203 ± 20 μM, $n = 18$) and FW (193 ± 71 μM, $n = 32$) compared to RW (154 ± 47 μM, $n = 20$; pairwise *t* test, $p = 0.03$ and $p = 0.05$, respectively). In Year 2, no differences were found between HW (81 ± 38 μM, $n = 21$) and FW (96 ± 64 μM, $n = 21$), but mean surface CO₂ concentrations measured in those periods were consistently lower than the values measured in HW and FW periods of the first year of study (pairwise *t* test, $p < 0.001$; Table 1).

CO₂ fluxes and k_{600} for both sites varied with the phase of the hydrological cycle based on one-way ANOVA. At the WE site, CO₂ fluxes ($F(2,55) = 19$, $p < 0.001$) and values of k_{600} ($F(2,55) = 17$, $p < 0.001$) tracked changes in the water level, with greater mean values observed during high water (29 ± 14 mmol m⁻² hr⁻¹ and 11 ± 4 cm hr⁻¹, $n = 19$) relative to rising (9 ± 8 mmol m⁻² hr⁻¹ and 5 ± 2 cm hr⁻¹, $n = 14$) and FW

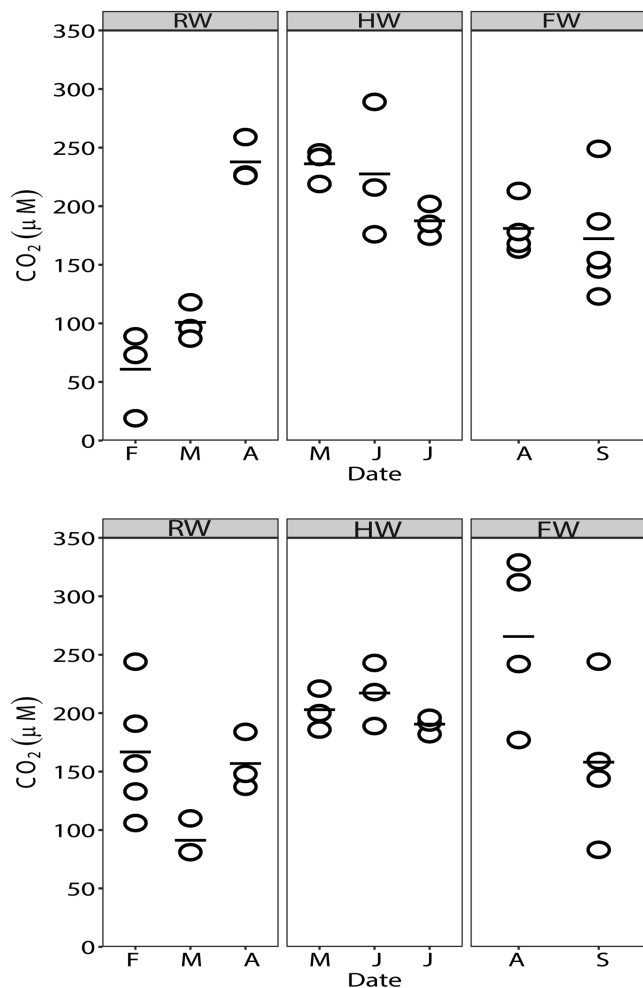


Figure 2. CO₂ concentrations measured at the wind-exposed site (WE, upper panel) and wind-protected site (WP, lower panel) for hydrological phases: rising water (RW), high water (HW) and falling water (FW). Horizontal bars represent the mean per sampling date, open circles represent each observation in a 24 hr period.

($9 \pm 7 \text{ mmol m}^{-2} \text{ hr}^{-1}$ and $5 \pm 4 \text{ cm hr}^{-1}$, $n = 25$; pairwise t test, $p < 0.001$; Figure 3). At the WP site, mean CO₂ fluxes ($F(4,107) = 16.2$, $p < 0.001$) were also higher during high water ($6 \pm 3 \text{ mmol m}^{-2} \text{ hr}^{-1}$, $n = 18$) compared to FW ($4 \pm 2 \text{ mmol m}^{-2} \text{ hr}^{-1}$, $n = 32$) but similar to mean values encountered during rising water ($6 \pm 4 \text{ mmol m}^{-2} \text{ hr}^{-1}$, $n = 20$) of Year 1 (pairwise t test, $p = 0.001$; Figure 3). Differences in mean k_{600} between periods of the hydrological cycle ($F(4,107) = 4.6$, $p = 0.002$) were higher when comparing the rising water ($3 \pm 2 \text{ cm hr}^{-1}$, $n = 20$) and high water periods ($3 \pm 1 \text{ cm hr}^{-1}$, $n = 18$) against the FW period ($2 \pm 1 \text{ cm hr}^{-1}$, $n = 32$) in Year 1 (pairwise t test, $p = 0.01$ and $p = 0.02$, respectively). In Year 2, mean CO₂ fluxes for a given period of the hydrological cycle were consistently lower than the mean values measured in all periods of Year 1 at the WP site (pairwise t test, $p < 0.001$; Table 1). For k_{600} , the FW period of Year 2 was similar to the FW period of Year 1 (pairwise t test, $p = 0.99$) and also lower than high water (pairwise t test, $p = 0.03$) and rising water periods (pairwise t test, $p = 0.02$) of Year 1 (Table 1).

Day–night differences were statistically different for CO₂ fluxes when comparing all measurements at both sites (paired t test, $t(11) = 3.8$, $p = 0.003$). When differentiating between WP and WE sites, mean CO₂ concentrations were numerically lower during the day (WP = $128 \pm 68 \text{ μM}$, $n = 33$, and WE = $166 \pm 56 \text{ μM}$, $n = 13$) compared to the night (WP = $172 \pm 72 \text{ μM}$, $n = 20$, and WE = $183 \pm 74 \text{ μM}$, $n = 14$) at both sites, although they were not statistically different (paired t test, WP: $t(11) = -0.63$, $p = 0.54$; WE: $t(7) = -0.4$, $p = 0.7$). CO₂ fluxes and k_{600} were statistically different only for the WP site. CO₂ fluxes (paired t test, $t(11) = 2.7$, $p = 0.02$) and k_{600} (paired t test, $t(11) = 2.7$, $p = 0.02$) were lower during the night ($3.6 \pm 2.6 \text{ mmol m}^{-2} \text{ hr}^{-1}$ and $2 \pm 0.5 \text{ cm hr}^{-1}$, $n = 42$) compared to the day ($3.9 \pm 3.3 \text{ mmol m}^{-2} \text{ hr}^{-1}$ and $3 \pm 2 \text{ cm hr}^{-1}$, $n = 70$; Figure 4) and consistent with day–night differences at this site for wind speeds that were also higher during the day compared to the night (unpaired t test, $t(51) = 3.5$, $p = 0.0009$). Although not significantly different, we found numerically higher mean values for CO₂ fluxes and k_{600} during the night ($20 \pm 17 \text{ mmol m}^{-2} \text{ hr}^{-1}$ and $8 \pm 5 \text{ cm hr}^{-1}$, $n = 29$) compared to the day ($12 \pm 9 \text{ mmol m}^{-2} \text{ hr}^{-1}$ and $6 \pm 4 \text{ cm hr}^{-1}$, $n = 29$) at the WE site. Wind differences at this site followed the same trend as for the

WP site with higher wind speeds during the day (unpaired t test, $t(24) = 2.2$, $p = 0.04$), but the higher fluxes during the night were associated with vertical mixing (Figure 5).

3.2. Environmental Variables and Relationships with CO₂ Concentrations

Environmental variables varied with water level. When depths were low during rising and FW, Chl-*a*, DO, TN, TSS, conductivity, and temperatures were higher compared to high water. Average hourly wind records prior to CO₂ flux measurements varied from below detection to 2.2 m s^{-1} at the WP site and from 0.3 to 5.1 m s^{-1} at the WE site (frequency distributions are given in Figure S2). Environmental variables for both sites are summarized in Table S1.

DO was strongly inversely correlated to CO₂ concentrations ($n = 80$, $r^2 = -0.86$, $p < 0.001$). We identified one outlier among our environmental variables. The outlier was high Chl-*a* and high CO₂ concentrations that occurred at the WP site during the FW in 2015. At that time, the thermocline deepened causing upwelling of nutrient-enriched waters that caused an increase in Chl-*a*, and water enriched in CO₂ concentration was upwelled that raised CO₂ concentrations. DO was the only environmental predictor that was retained from the multimodel selection procedure. It has an AICc value of 149.9 and explained around 90% (marginal R^2) or 97% (conditional R^2) variability in surface CO₂ concentration.

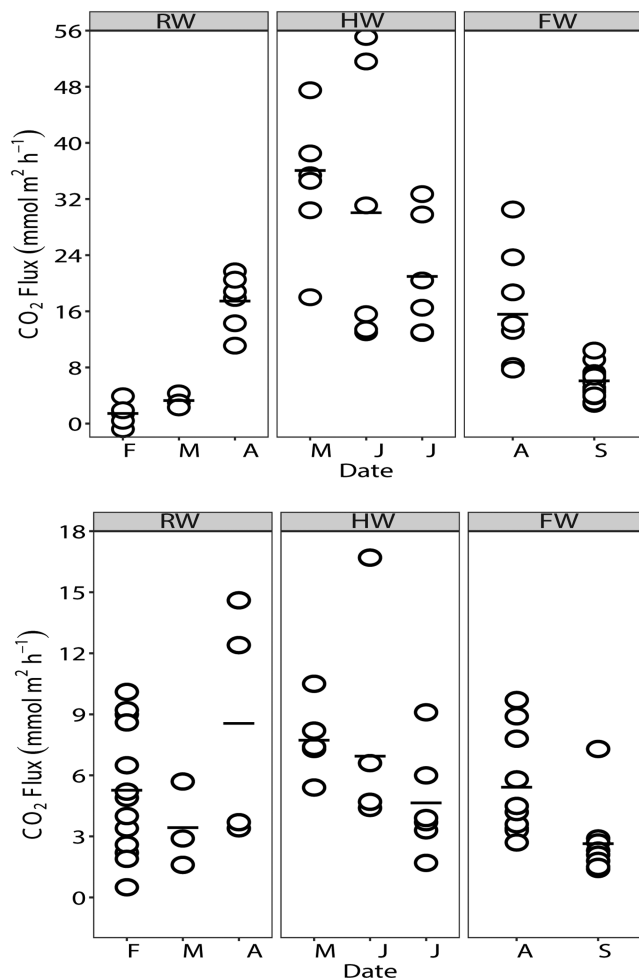


Figure 3. CO₂ evasion measured at the wind-exposed site (WE, upper panel) and wind-protected site (WP, lower panel) for hydrological phases: rising water (RW), high water (HW) and falling water (FW). Horizontal bars represent the mean, open circles represent each observation in a 24 hr period. Note differences in scale of y axis between sites.

3.3. Spatial and Seasonal Integration of CO₂ Fluxes

The WP forests in the northern Janauacá floodplain had a total area of 94 km², which corresponds to 88% of the total area of floodable forest estimated for this part of the lake. The remaining 12% is attributed to areas with WE forests.

The maximum likelihood estimator of the flux for all inundated forests in the Janauacá floodplain is 45 Gg-C yr⁻¹ with CI of 31 to 69 Gg-C yr⁻¹. Emissions from sheltered forests represent 31 Gg-C yr⁻¹ with CI of 21 to 49 Gg-C yr⁻¹ and those from wind-exposed forests 14 Gg-C yr⁻¹ with CI of 10 to 20 Gg-C yr⁻¹. These values were almost the same based on calculations per month and for data lumped into hydrological periods.

We obtained a regional estimate based on the area of flooded vegetation and open water during high and low water for a sequence of reaches along the Solimões and Amazon rivers in the central Amazon basin using data in Melack and Hess (2010). From Marañón to Gurupá, their high water area of flooded forests, woodlands, and shrubs (52,700 km²) combined with our high water estimates of CO₂ flux, using the proportional areas of wind-sheltered and wind-exposed forest calculated for Janauacá, yields a total high water flux of 133 ± 65 Tg-C for these reaches. When extrapolated to the total high water area of flooded forests, woodlands, and shrubs for the lowland basin (630,000 km²; Melack & Hess, 2010), the total high water flux is $1,590 \pm 780$ Tg-C.

4. Discussion

4.1. Diel, Seasonal, and Spatial Variability of CO₂ Concentrations and Fluxes

As we hypothesized, the WE site near a large area of open water had higher CO₂ fluxes and k values compared to the more sheltered WP site. This result is related to the increased advection, mixing, and turbulence occurring in sites near large open water areas. Daily fluxes measured in our study are higher than or similar to the few other measurements in waters within tropical and subtropical flooded forests (Table 2). This finding supports our suggestion that flooded forests have high rates of CO₂ evasion to the atmosphere and make a large contribution to regional CO₂ evasion in the Amazon basin.

While our time series data support previous studies that CO₂ concentrations and fluxes vary seasonally, the frequency of our measurements further illustrated that variability was high at each site and during each measurement period. We corroborate previous studies reporting higher CO₂ concentrations and fluxes during the high water period for Amazonian rivers (Almeida et al., 2017; Amaral et al., 2019; Devol et al., 1995; Richey et al., 1990) and floodplain lakes (Abril et al., 2014; Rudorff et al., 2011). The seasonal pattern can be explained by (i) increases in water depth that increase depth integrated respiration (Devol et al., 1995; Forsberg et al., 2017) and (ii) the extent of inundation of the floodplains. CO₂ concentrations in floodplains are positively related to the area of inundated vegetated habitats (Abril et al., 2014; Amaral et al., 2019; Borges et al., 2015) that are greater during the high water period (Melack & Hess, 2010). The vegetated habitats contribute particulate organic carbon and DOC to the floodplains that can be decomposed in situ, generating CO₂ and CH₄, buried in the sediments or transported laterally to the rivers (Engle et al., 2008; Melack & Engle, 2009; Melack & Forsberg, 2001; Richey et al., 1988, 1990). Additionally, they contribute CO₂ to floodplain waters via root respiration (Hamilton et al., 1995; Piedade, Ferreira, et al., 2010).

Day–night differences were one source of the variability but were statistically significant only for CO₂ fluxes and k_{600} at the WP site with higher mean values during the day. Wind-induced currents or internal waves within the stratified waters of the flooded forests and neighboring habitats may have transported or mixed

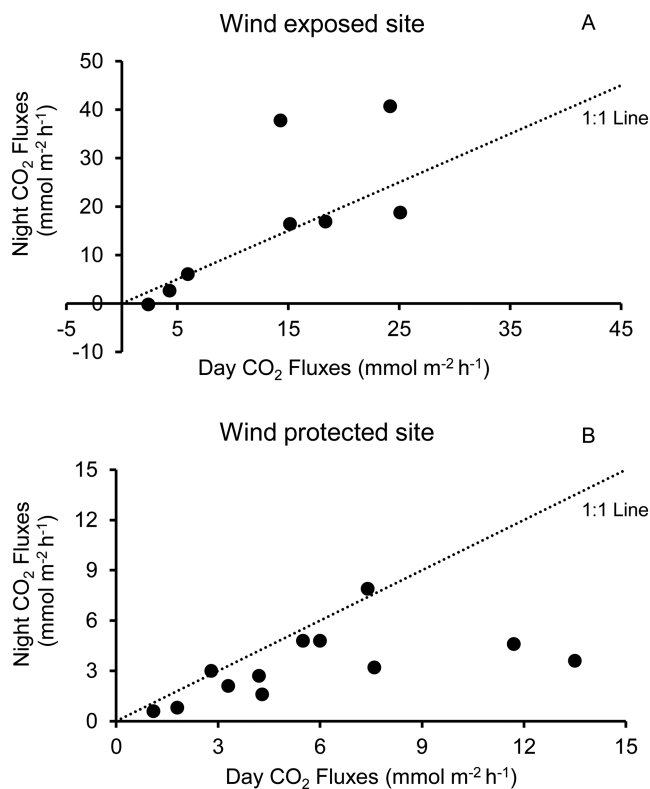


Figure 4. Mean CO₂ fluxes measured during the night versus measurements made during the day for the (a) wind-exposed and (b) wind-protected sites. Dashed lines represent the 1:1 lines.

tion into the flooded forests. Thus, between year differences in the hydrological conditions contribute to variability.

The interannual differences have implications for understanding possible impacts of climate change in tropical floodplains. For example, extreme events are increasing in frequency in the Amazon basin (Marengo & Espinoza, 2016), and projected climate change scenarios indicate reductions in the extent of inundated areas during the low water period (Sorribas et al., 2016), similar to our observations in Year 2. Our results support a reduction in CO₂ concentrations and fluxes from flooded forests under this scenario. However, we did not measure the fluxes from exposed sediments. Evidence from other studies in flooded forests in tropical (Tathy et al., 1992) and temperate (Happell & Chanton, 1993; Pulliam, 1993) zones reports positive CO₂ fluxes from nonflooded sediments in the floodable forest. However, Dalmagro et al. (2019) reported CO₂ fluxes ingassing during flooded season and outgassing during dry season in a study in seasonally inundated forests of the Pantanal floodplain. Additional measurements from exposed sediments during the noninundated phase are needed to allow a better evaluation of the impacts of variations in inundation periods.

4.2. Inverse Relation Between CO₂ Concentrations and DO

An inverse relation between CO₂ concentrations and DO was observed in this study as in many freshwater ecosystems, including tropical floodplains along sub-Saharan African rivers (Borges et al., 2015), the Pantanal (Hamilton et al., 1995), and temperate swamp forests (Happell & Chanton, 1993). In the Pantanal wetlands, the highest CO₂ concentrations and fluxes occurred as flooding began because of decomposition of freshly inundated soil and plant organic matter (Dalmagro et al., 2018; Hamilton et al., 1997). The inverse relation between CO₂ concentrations and DO suggests that aerobic processes are important for CO₂ production. Sediment respiration (Cardoso et al., 2013), methane oxidation (Barbosa et al., 2018), and planktonic respiration (Amaral et al., 2018; Waichman, 1996; Ward et al., 2013) are all processes that consume DO and produce dissolved CO₂.

water with elevated CO₂ concentrations into the surface waters within the flooded forest. Near-surface turbulence in the forest may have increased in the day due to advective flows generated outside the forest and higher wind speeds resulting in higher gas transfer velocities (MacIntyre et al., 2019). Values of k_{600} under these conditions will be higher than those expected from convection at night when winds are negligible. At the WE site, values were similar during the day and night except on two occasions when fluxes at night were nearly twice those in the day (Figure 4a). These occurred during high water in May and June 2015 when water depths were 5 to 7 m, depths where CO₂ did accumulate, and anoxia developed because stratification can persist. The actively mixing layer increased from 1.2 to 6 m at night, as indicative of mixing, and surface CO₂ concentrations increased (Figure 5). Fluxes increased as a result.

The variability of k_{600} was higher at the WE site as were mean values (6.7 ± 4.6 SD) relative to the WP site (2.3 ± 1.6 SD; Figure S3). The higher k_{600} values are likely associated with increases in shear in the surface waters of the flooded forest caused by wind-induced water currents from nearby open water (MacIntyre et al., 2019). Ho et al. (2018) obtained similar results in the Everglades.

Between year variability in surface water CO₂ concentrations occurred at the WP site. Values were higher in Year 1, likely because of more extensive and a longer inundation. Additionally, floating macrophytes whose decay and root respiration contributes to CO₂ in the water column (Hamilton et al., 1995; Mortillaro et al., 2016; Waichman, 1996) were present in Year 1 but not in Year 2. Advective flows can transport this water with higher gas concentra-

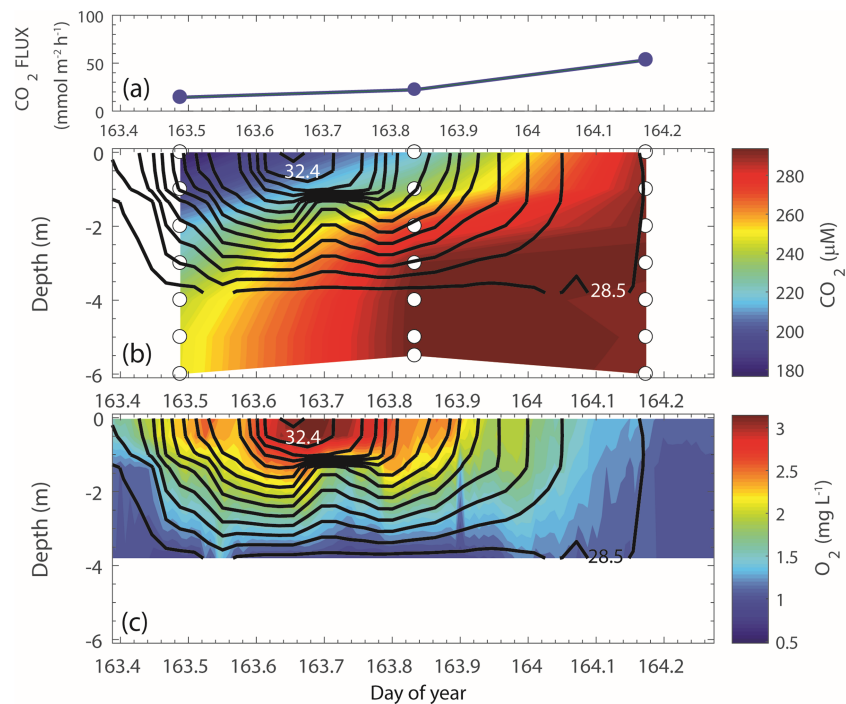


Figure 5. (a) time series of CO₂ fluxes, (b) dissolved CO₂ concentrations from discrete measurements at depths indicated by white dots, and (c) 10 min averaged time series of dissolved oxygen in the wind-exposed flooded forest in June 2015. Hourly averaged isotherms at 0.3 °C intervals are shown as black contours with maximum and minimum isotherms labelled.

More CO₂ was produced at our sites than expected by aerobic respiration within the water column (Figure 6). If aerobic respiration and CO₂ production were in balance, the excess of CO₂ (Ex-CO₂, i.e., CO₂ in the water subtracted from equilibrium CO₂ saturation) and the apparent oxygen utilization (AOU, i.e., atmospheric equilibrium O₂ solubility subtracted from the O₂ concentration measured in surface water)

would follow a 1:1 line. Processes that could cause increased CO₂ production or elevated Ex-CO₂ include methanogenesis (Bartlett et al., 1988), groundwater CO₂ inputs, and root respiration within the flooded forest and associated herbaceous plants that use atmospheric CO₂ in photosynthesis and release respired CO₂ through their inundated roots (Abril et al., 2014; Abril & Borges, 2019; Melack et al., 2009; Piedade, Junk, et al., 2010). The first two processes were not likely to be important at our sites. Ex-CO₂ was not correlated with methane measured at these sites (Barbosa, 2018; $p > 0.05$, $r^2 = 0.0063$, slope = 0.0019), and the contribution of groundwater to the hydrologic balance is less than 1% in Janauacá (Bonnet et al., 2017).

The Ex-CO₂ vs AOU relation in our study is similar to the relation reported for the Solimões River and other Amazon waters (Devol et al., 1995; Richey et al., 1988). These studies suggested the importance of lateral floodplains as sites for CO₂ production and sources to the rivers. This hypothesis was examined by Abril et al. (2014), who used a one-dimensional model for CO₂ transport by the Amazon River to demonstrate that CO₂ from floodplains could be transported downstream over hundreds of kilometers. Further evidence of inputs of labile organic carbon to the rivers from floodplains is provided by measurements in the eastern Amazon by Moreira-

Table 2
Average CO₂ Diffusive Flux (FCO₂) Measured Within Flooded Forests From Different Studies

Location	Forest type	Method	FCO ₂ mg C·m ⁻² d ⁻¹
Amazon basin ^a	Floodplain	Chamber	343
Florida, USA ^b	Swamp	Chamber	973 ± 599
Georgia, USA ^c	Floodplain	Chamber	115 – 1270
Congo basin ^d	Floodplain	Chamber	2,640 ± 1,370
Pantanal, Brazil ^e	Floodplain	Modeled	320
Northern Australia ^f	Floodplain	Chamber	1,260 ± 1,258
Amazon basin ^g	Floodplain	Chamber	2,182 ± 2,954

^aDevol et al. (1988). Mean value calculated from nine measurements made during the high-water period. ^bHappell and Chanton (1993). Mean value calculated from single daytime measurements once a month for 1 year. ^cPulliam (1993). Range of mean daily fluxes obtained from ten transects with three measurements done at a monthly frequency for a 2-year period. ^dTathy et al. (1992). Mean value from eleven daily measurements made in flooded forests. ^eDalmagro et al. (2018). Mean value obtained using 40 measurements of surface CO₂ water concentrations and a wind-based equation during the flooded season (March to June). ^fBass et al. (2014). Mean value obtained from seven sites with daily replicate measurements done eight times during the flood season (February to May). ^gThis study. Mean value from two sites with multiple measurements over diel cycles in 12 monthly campaigns distributed through two hydrological years when the forest sites were flooded and accessible.

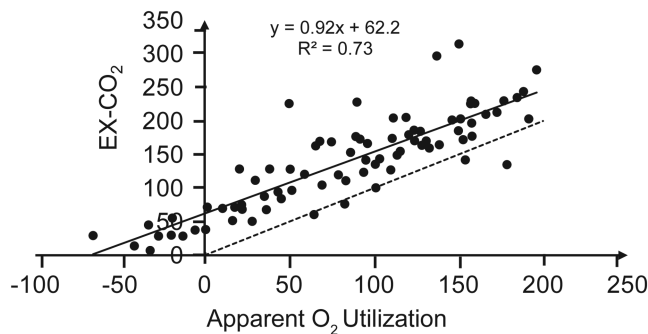


Figure 6. Excess of CO_2 as function of apparent oxygen utilization (AOU) in μM , calculated for near-surface waters of inundated forests. Dashed line is the 1:1 line, and solid black line is the regression line.

study reported nine CO_2 measurements made in July and August 1985 in flooded forests fringing open water areas, similar to our WE site (Devol et al., 1988). The range of values in that study, $466\text{--}2,400 \text{ mg C}\cdot\text{m}^{-2} \text{ d}^{-1}$, is lower than the range, $3,706\text{--}15,867 \text{ mg C}\cdot\text{m}^{-2} \text{ d}^{-1}$, ($n = 19$) observed during a comparable period of our study, high water at the WE site.

Mean daily fluxes measured in our study ($2,182 \pm 2,954 \text{ SD mg C}\cdot\text{m}^{-2} \text{ d}^{-1}$) are higher than or similar to the few other measurements in waters within tropical and subtropical flooded forests (Table 2). The low CO_2 efflux reported by Dalmagro et al. (2018) is likely related to their use of a wind-based equation to estimate the CO_2 fluxes. While wind speeds in flooded forest sites are low, other processes can increase fluxes, as noted above and in MacIntyre et al. (2019). The large range in our study indicates the need for a sampling over diel cycles on a seasonal basis (Table 2).

Seasonally inundated and riparian forests are the main aquatic habitat within the lowland Amazon basin (Hess et al., 2015; Junk et al., 2010; Melack & Hess, 2010). Most of these forests are likely to be more similar to our WP site, as the open water areas in the lowland Amazon basin corresponds to only 8% of the total basin area (Melack & Hess, 2010). Inundated forests vary in distribution and floristic composition depending on fluvial geomorphology, flooding regimes, and soil and water qualities (Junk et al., 2010). CO_2 fluxes among these forest types are likely to vary.

We report a total high water flux, integrated to the area of flooded forests, woodlands, and shrubs during this period, for the lowland Amazon of $1,590 \pm 777 \text{ Tg C}$. For comparison, Melack and Hess's (2010) estimate of open water in rivers and lakes at high water ($64,700 \text{ km}^2$) and the mean CO_2 fluxes reported mainly for rivers by Amaral et al. (2019; $4.7 \text{ g C}\cdot\text{m}^{-2} \text{ d}^{-1}$) and Richey et al. (1990; $5.2 \text{ g C}\cdot\text{m}^{-2} \text{ d}^{-1}$) yields a total high water flux from open water of 320 Tg C . Since fluxes from lakes are often less than from rivers (Melack, 2016; Polsenaere et al., 2013; Rudorff et al., 2011), this estimate for open water is likely high. At low water, Melack and Hess (2010) estimated that flooded forests, woodlands, and shrubs covered $17,270 \text{ km}^2$ of the mainstem reaches. To provide annual estimates will require time series of inundated habitats derived from hydrological models and remote sensing analysis, such as those done by Arnesen et al. (2013) and Ferreira-Ferreira et al. (2015) that map the duration of inundation of flooded forests distributed throughout the Amazon basin. Measurements of CO_2 fluxes from other types of flooded forests are also essential.

Regional estimates of CO_2 fluxes offered by Richey et al. (2002) and Melack (2016) did not include data from flooded forests. Melack's (2016) estimate for floodplains and wetland habitats used an average $p\text{CO}_2$ value ($335 \mu\text{M}$; $10,900 \mu\text{atm}$) from Richey et al. (2002) and k_{600} of 12 cm hr^{-1} from studies in lakes. Our lower k_{600} values for flooded forests, a large component of floodplain and wetland habitats, clearly indicate a lower overall flux than suggested in Melack (2016). Richey et al. (2002) selected a k_{600} of 2.7 cm hr^{-1} as a conservative value for floodplains and lakes. Though low for lakes, this value is similar to our k_{600} values for sheltered flooded forests. As a consequence, their regional estimate, if expressed as $\text{mmol C}\cdot\text{m}^{-2} \text{ d}^{-1}$ (189 ± 55), is similar to our mean value (182 ± 247) for flooded forests on the Janauacá floodplain. These new estimates highlight the importance of flooded forests for the carbon budget of the Amazon basin and the need for more studies in these aquatic habitats.

Turcq et al. (2013). Moreover, Richey et al. (1990) suggested that aquatic and terrestrial macrophytes and flooded forests in floodplains were likely sources of labile organic C for the mainstem river.

We also observed negative AOU values that represent times when photosynthetic oxygen production exceeded respiration within the flooded forests. The negative AOU values occurred when water depths were 1.5 to 3.5 m and DO concentrations were 7.4 to 9.3 mg L^{-1} in the flooded forest sites. These concentrations were similar to those observed in nearby open water.

4.3. Implications for the Regional C Budget and Other Forested Wetlands

To our knowledge, we provide the first multiseason study of CO_2 concentrations and fluxes in flooded forests for the Amazon basin. The one prior

Seasonally inundated forests in the Amazon and elsewhere occur in an aquatic–terrestrial transition zone that includes other aquatic habitats such as open waters and macrophytes. Integration of C fluxes in the ATTZ is challenging, as the aquatic habitats are interconnected and interact with each other. For comparison, we contrast our mean CO₂ evasion with an estimate of net primary production (NPP) of 1,150 Mg C·km^{−2}·yr^{−1} for flooded forests in the central Amazon basin (Melack & Forsberg, 2001; Worbes, 1997). This rate is based on 30% of the live wood increment, fine litter, and large woody detritus inputs to the aquatic system. Our mean CO₂ evasion (590 Mg C·km^{−2}·yr^{−1}) is about half of the NPP estimate, considering that these forests remain flooded for 270 days a year. The excess of C inputs from NPP corroborates findings by other studies that argue for the mixed C sources to supply CO₂ evasion rates in open waters of the Amazon basin (Engle et al., 2008; Melack & Forsberg, 2001; Quay et al., 1992; Ward et al., 2013, 2016).

We suggest that C studies in aquatic habitats of ATTZ integrate C fluxes by weighting their relative areal coverage in the floodplain. This practice will avoid overrepresentation of recent floodplain CO₂ flux estimates (e.g., de Ramera et al., 2013; Melack, 2016) that are based mainly on data obtained from open water habitats but extrapolated to areas that encompass other aquatic habitats with different characteristics and typically lower emissions, such as flooded forests and floating macrophytes. Future studies in flooded forests should aim to improve estimates of tree stem CO₂ fluxes as well as fluxes from soil when these forests are not inundated.

Abril and Borges (2019) review the conceptual framework of carbon fluxes in the terrestrial aquatic continuum and highlight the need for including flooded land as a component in this continuum. They propose that C fluxes from flooded lands should be treated as a transport term between upland and inland waters. An example of their conceptual framework is provided by an organic carbon budget developed by Melack and Engle (2009) for an Amazon floodplain lake. More C budgets studies in flooded lands are needed as the basis for modeling studies as well as to provide correct comparisons between the terrestrial and aquatic C fluxes.

The results from our study demonstrate the importance of combining gas measurements with meteorological and limnological information to understand CO₂ fluxes in flooded forests. Additional direct measurements of *k* and studies of the mechanisms that generate turbulence and effects on *k*₆₀₀ under low wind speed conditions are needed. We recommend that further studies include measurements throughout the day and night. The contrasting *k* and CO₂ fluxes values observed in sheltered flooded forests versus wind-exposed forests should be considered in the integration of CO₂ fluxes in forested wetlands.

Data Statement

Data were deposited in the KNB data repository operated by NCEAS and assigned a DOI:10.5063/F1CR5RPD (<https://doi.org/10.5063/F1CR5RPD>).

No authors have financial conflicts of interest.

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