Carbon dioxide fluxes to the atmosphere from waters within flooded forests in the Amazon basin

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Key Points:

- CO_2 concentrations in near-surface waters within flooded Amazon forests ranged from 19 to 329 µM, and CO_2 fluxes from -0.8 to 55 mmol m^{-2} h^{-1}.

- Daytime CO_2 fluxes were higher at a wind protected site, while night-time fluxes were often higher at a wind exposed site.

- On an areal basis CO_2 fluxes from flooded forests during high water levels are the major contributor among aquatic habitats

Abstract

Inundated tropical forests are under-represented 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 CO_2 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). CO_2 profiles and estimates of air-water gas exchange were combined with ancillary environmental measurements. Surface CO_2 concentrations ranged from 19 to 329 μM, CO_2 fluxes ranged from -0.8 to 55 mmol m^{-2} h^{-1} and gas transfer velocities ranged from 0.2 to 17 cm h^{-1}. CO_2 concentrations and fluxes were highest during the high water period. CO_2 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. CO_2 concentrations and fluxes were lower at the WP site following an extended period of exceptionally low water. The CO_2 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 ± 247 mmol m^{-2} 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 (CO_2). However, information on CO_2 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 CO_2 exchanges within flooded forests of the central Amazon basin. Our approach combines measurement of dissolved CO_2 concentrations and fluxes between the water and atmosphere and ecological data. Although the rates of CO_2 emission by flooded forests are lower than other aquatic habitats, such as open waters in rivers and lakes, the combination of high CO_2 concentrations and a large area results in an appreciable regional out-gassing 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.

Keywords: tropical, CO_2 evasion, wetlands, floodplains

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 (Lehner & Döll, 2004; Cole et al., 2007; Raymond et al., 2013). Tropical freshwater systems are under-represented 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 CO_2 to floodplains and rivers (Worbes, 1997; Melack & Forsberg, 2001; Melack & Engle, 2009), and contribute to evasion of CO_2 and methane from these aquatic environments (Richey et al., 2002; Melack et al., 2004; Abril et al., 2014; Melack, 2016; Pangala et al., 2017). However, almost all studies of CO_2 outgassing from Amazon floodplains have been restricted to open water areas.

CO_2 exchanges with the atmosphere are determined by the gradient of water-air CO_2 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 & Melack 1995; MacIntyre et al., 2002; Tedford et al., 2014; MacIntyre et al., 2018), 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 CO_2 concentration gradients, and meteorological parameters in flooded forests are needed to better understand the mechanisms associated with CO_2 outgassing from these aquatic habitats and to evaluate their role in the carbon cycle.

The first regional estimate of CO_2 outgassing for the aquatic habitats of the Amazon basin (Richey et al., 2002) reported CO_2 outgassing of 830 ± 240 Mg C km^{-2} y^{-1}. Subsequent measurements conducted in lakes (Rudorff et al., 2011; Polsenaere et al., 2013), reservoirs (Kemenes et al., 2011) and rivers (Alin et al., 2011; 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 CO_2 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 CO_2 dynamics in inundated forests, the largest aquatic habitat in the Amazon basin, but the one least studied. We report CO_2 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 CO_2 fluxes in the forests. 2) Wind protected forests will have lower *k* values and consequently lower CO_2 fluxes than wind exposed sites. 3) Flooded forests have high rates of CO_2 evasion to the atmosphere and make a large contribution to regional CO_2 evasion in the Amazon basin.

2. Methods

2.1 Site description and sampling

Measurements over two 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 aquatic terrestrial transition zone (ATTZ) (Worbes 1997; Parolin et al., 2010). Phenological behavior is largely associated with the time and extent of inundation, and evergreen, semi-deciduous and deciduous species shred 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 (Melack & Forsberg 2001; Melack et al., 2009; Bonnet et al. 2017).

Measurements of carbon dioxide partial pressure (pCO_2) and CO_2 emissions were made when the sites were flooded and accessible at multiple times of the day and night. Measurements were made on 12 occasions 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).

2.2 - Analytical methods

pCO_2 was measured with an off-axis integrated cavity output spectrometer (Ultraportable Greenhouse Gas Analyzer (UGGA), 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 UGGA. All measurements were made in replicate as ~10-minute 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

mmol m^{-2} h^{-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 = $k[\Delta CO_2]$ using our measurements of CO_2 fluxes (F) and the difference between observed and equilibrium gas concentrations (ΔCO_2) derived from the pCO_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 & Guinasso (1979) to calculate concentration. Estimated k values were normalized to 20ºC (k_{600}) for which 600 is the Schmidt number for CO_2 at 20ºC and Sc at other temperatures were obtained from Wanninkhof (1992).

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 0.002ºC accuracy (RBRsolo) recording every 0.5 s, and with optical dissolved oxygen sensors (PME MiniDOT loggers) recording every 10 minutes (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 & 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 h) glass fiber GF/F filters (Whatman), collected in pre-cleaned (10% HCl wash, deionized water rinse) and pre-combusted (450–500°C for 1 h) 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 (DEM) 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 multi-resolution 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 DEM 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) wind-exposed flooded forest (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 y^{-1}) from the flooded forests in the northern region of Janauacá an expression similar to that in Melack et al. (2004) was used:

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

f is the mean daily flux of CO_2 for each month and site (g C m^{-2} d^{-1}), A is flooded forest area for each month (km^2), 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 re-sampled 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 *bootstrp* 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

CO_2 concentration, k_{600}, and CO_2 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 CO_2 concentrations were normally distributed, but k_{600} and CO_2 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 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 h into categories of day (6:00 am to 6:00 pm) and night (6:00 pm to 6:00 am) to evaluate the implications of sampling time for CO_2 fluxes, variability of k_{600}, and CO_2 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 CO_2 concentrations measured in flooded forests with contrasting wind exposure, we applied a multi-model 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 CO_2 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), ΔAICc, and AICc model weights (wi) 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 ΔAICc of the 'best' model. We calculated a daily geometric mean of CO_2 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, 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 co-linear 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 (*wi*) 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, i.e., by summing the weights of models where each variable appears (Grueber et al., 2011, Galipaud et al., 2014). 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 - CO_2 concentrations and fluxes

Surface CO_2 concentrations ranged from 19 to 329 µM (pCO_2 = 664 to 11006 µatm); the overall geometric mean was 134 µM, and the mean and standard deviation were 155 ± 71 µM (pCO_2 = 4465; 5117 ± 2326 µatm) (Table 1). 170 measurements of CO_2 flux were made at the two flooded forests sites, and fluxes ranged from -0.8 to 55 mmol m^{-2} h^{-1} with an overall mean and standard deviation of 7.8 ± 10.1 mmol m^{-2} h^{-1} (Table 1). Gas transfer velocities derived from these measurements ranged from 0.2 to 17 cm h^{-1} with an overall geometric mean value of 2.6 cm h^{-1} and mean and standard deviation of 3.8 ± 3.6 cm h^{-1} (Table 1). Mean CO_2 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). CO_2 fluxes and k_{600} were greater at the WE site (16 ± 14 mmol m^{-2} h^{-1} and 6.7 ± 4.6 cm h^{-1}) compared to the WP site (5 ± 3 mmol m^{-2} h^{-1} and 2.4 ± 1.7 cm h^{-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 CO_2 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 falling water (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 one, the CO_2 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 two, no differences were found between

HW (81 ± 38 µM, n=21) and FW (96 ± 64 µM, n=21), but mean surface CO_2 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).

CO_2 fluxes and k_{600} for both sites varied with the phase of the hydrological cycle based on one-way ANOVA. At the WE site, CO_2 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} h^{-1} and 11±4 cm h^{-1}, n=19) relative to rising (9 ± 8 mmol m^{-2} h^{-1} and 5 ± 2 cm h^{-1}, n=14) and falling water (9 ± 7 mmol m^{-2} h^{-1} and 5 ± 4 cm h^{-1}, n=25) (Pairwise t-test, p<0.001)(Figure 3). At the WP site, mean CO_2 fluxes (F(4,107)=16.2, p<0.001) were also higher during high water (6±3 mmol m^{-2} h^{-1}, n=18) compared to falling water (4 ± 2 mmol m^{-2} h^{-1}, n=32) , but similar to mean values encountered during rising water (6 ± 4 mmol m^{-2} h^{-1}, n=20) of year one (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 ± 2 cm h^{-1}, n=20) and high water periods (3 ± 1 cm h^{-1}, n=18) against the falling water period (2 ± 1 cm h^{-1}, n=32) in year one (Pairwise t-test, p=0.01 and p=0.02, respectively). In year two, mean CO_2 fluxes for a given period of the hydrological cycle were consistently lower than the mean values measured in all periods of year one at the WP site (pairwise t-test, p<0.001) (Table 1). For k_{600} the falling water period of year two was similar to the falling water period of year one (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 one (Table 1).

Day-night differences were statistically different for CO_2 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 CO_2 concentrations were numerically lower during the day (WP=128 ± 68 µM, n=33, and WE=166 ± 56 µM, n=13) compared to the night (WP=172 ± 72 µM, n=20, and WE=183 ± 74 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=0.74). CO_2 fluxes and k_{600} were statistically different only for the WP site. CO_2 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 ± 2.6 mmol m^{-2} h^{-1} and 2 ± 0.5 cm h^{-1}, n=42) compared to the day (3.9 ± 3.3 mmol m^{-2} h^{-1} and 3 ± 2 cm h^{-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 CO_2 fluxes and k_{600} during the night (20 ± 17 mmol m^{-2} h^{-1} and 8 ± 5 cm h^{-1}, n=29) compared to the day (12 ± 9 mmol m^{-2} h^{-1} and 6 ± 4 cm h^{-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 CO_2 concentrations

Environmental variables varied with water level. When depths were low during rising and falling water, Chl-*a*, DO, TN, TSS, conductivity and temperatures were higher compared to high water. Average hourly wind records prior to CO_2 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 supporting information (Table S1).

DO was strongly inversely correlated to CO_2 concentrations (n=80, r^2= -0.86, p<0.001). We identified one outlier among our environmental variables. The outlier was high chlorophyll and high CO_2 concentrations that occurred at the WP site during the falling water in 2015. At that time, the thermocline deepened causing upwelling of nutrient-enriched waters that caused an increase in chlorophyll, and water enriched in CO_2 concentration was upwelled that raised CO_2 concentrations. DO was the only environmental predictor that was retained from the multi-model 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 CO_2 concentration.

3.3 - Spatial and seasonal integration of CO_2 fluxes

The WP forests in the northern Janauacá floodplain had a total area of 94 km^2, 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 y^{-1} with CI of 31 to 69 Gg C y^{-1}. Emissions from sheltered forests represent 31 Gg C y^{-1} with CI of 21 to 49 Gg C y^{-1} and those from wind exposed forests 14 Gg C y^{-1} with CI of 10 to 20 Gg C y^{-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 & Hess (2010).

From Marañón to Gurupá their high water area of flooded forests, woodlands and shrubs (52,700 km^2) combined with our high water estimates of CO_2 flux, using the proportional areas of wind-sheltered and wind-exposed forest calculated for Janauacá, yields a total high water flux of 133 $\pm$ 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 km^2) (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 CO_2 concentrations and fluxes

As we hypothesized, the WE site near a large area of open water had higher CO_2 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 CO_2 evasion to the atmosphere and make a large contribution to regional CO_2 evasion in the Amazon basin.

While our time series data supports previous studies that CO_2 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 CO_2 concentrations and fluxes during the high water period for Amazonian rivers (Richey et al., 1990; Devol et al., 1995; Almeida et al. 2017; Amaral et al., 2019) and floodplain lakes (Rudorff et al., 2011; Abril et al., 2014). 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. CO_2 concentrations in floodplains are positively related to the area of inundated vegetated habitats (Abril et al., 2014; Borges et al., 2015; Amaral et al., 2019), 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 CO_2 and CH_4, buried in the sediments, or transported laterally to the rivers (Richey et al., 1988;1990; Melack & Forsberg, 2001; Engle et al., 2008; Melack & Engle, 2009). Additionally, they contribute CO_2 to floodplain waters via root respiration (Hamilton et al., 1995; Piedade et al., 2010a).

Day-night differences were one source of the variability but were statistically significant only for CO_2 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 water with elevated CO_2 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 CO_2 did accumulate, and anoxia developed because stratification can persist. The actively mixing layer increased from 1.2 m to 6 m at night, as indicative of mixing, and surface CO_2 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 $\pm$ 4.6 SD) relative to the WP site (2.3 $\pm$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 CO_2 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 CO_2 in the water column (Waichman, 1996; Mortillaro et al., 2016; Hamilton et al., 1995) were present in year 1 but not in year 2. Advective flows can transport this water with higher gas concentration 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 CO_2 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 (Pulliam, 1993; Happell & Chanton, 1993) zones report positive CO_2 fluxes from nonflooded sediments in the floodable forest. However, Dalmagro et al. (2019) reported CO_2 fluxes in-gassing 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 non-inundated phase are needed to allow a better evaluation of the impacts of variations in inundation periods.

4.2- Inverse relation between CO_2 concentrations and dissolved oxygen

An inverse relation between CO_2 concentrations and dissolved oxygen 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 CO_2 concentrations and fluxes occurred as flooding began because of decomposition of freshly inundated soil and plant organic matter (Hamilton et al., 1997; Dalmagro et al., 2018). The inverse relation between CO_2 concentrations and dissolved oxygen suggests that aerobic processes are important for CO_2 production. Sediment respiration (Cardoso et al., 2013), methane oxidation (Barbosa et al., 2018), and planktonic respiration (Waichman, 1996; Ward et al., 2013; Amaral et al., 2018) are all processes that consume dissolved oxygen and produce dissolved CO_2.

More CO_2 was produced at our sites than expected by aerobic respiration within the water column (Figure 6). If aerobic respiration and CO_2 production were in balance, the excess of CO_2 (Ex-CO_2, i.e., CO_2 in the water subtracted from equilibrium CO_2 saturation) and the apparent oxygen utilization (AOU, i.e., atmospheric equilibrium O_2 solubility subtracted from the O_2 concentration measured in surface water) would follow a 1:1 line. Processes that could cause increased CO_2 production or elevated Ex-CO_2

include methanogenesis (Bartlett et al., 1988), groundwater CO_2 inputs, and root respiration within the flooded forest and associated herbaceous plants that use atmospheric CO_2 in photosynthesis and release respired CO_2 through their inundated roots (Melack et al., 2009; Piedade et al., 2010b; Abril et al., 2014; Abril & Borges, 2019). The first two processes were not likely to be important at our sites. Ex-CO_2 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-CO_2 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 CO_2 production and sources to the rivers. This hypothesis was examined by Abril et al. (2014), who used a one-dimensional model for CO_2 transport by the Amazon River to demonstrate that CO_2 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-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 multi-season study of CO_2 concentrations and fluxes in flooded forests for the Amazon basin. The one prior 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 - 2400 mg C m^{-2} d^{-1}, is lower than the range, 3706 - 15867 mg C m^{-2} 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 (2182 $\pm$ 2954 SD mg C m^{-2} 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 (Junk et al., 2010; Melack & Hess, 2010; Hess et al., 2015). 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 ± 777 Tg C. For comparison, Melack & Hess's (2010) estimate of open water in rivers and lakes at high water (64,700 km^2) and the mean CO_2 fluxes reported mainly for rivers by Amaral et al. (2019; 4.7 g C m^{-2} d^{-1}) and Richey et al. (1990; 5.2 g C m^{-2} 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 (Rudorff et al., 2011; Polsenaere et al., 2013; Melack, 2016), this estimate for open water is likely high. At low water, Melack & Hess (2010) estimated that flooded forests, woodlands and shrubs covered 17,270 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 pCO_2 value (335 µM; 10900 µatm) from Richey et al. (2002) and k_{600} of 12 cm h^{-1} from studies in lakes. Our lower k_{600} values for flooded forests, a large component of floodplain and wetland habitats, clearly indicates a lower overall flux than suggested in Melack (2016). Richey et al. (2002) selected a k_{600} of 2.7 cm h^{-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 mmol C m^{-2} 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.

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 CO_2 evasion with an estimate of net primary production (NPP) of 1150 Mg C $km^{-2}y^{-1}$ for flooded forests in the central Amazon basin (Worbes 1997; Melack & Forsberg 2001). This rate is based on 30% of the live wood increment, fine litter, and large woody detritus inputs to the aquatic system. Our mean CO_2 evasion (590 MgC $km^{-2}y^{-1}$) 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 CO_2 evasion rates in open waters of the Amazon basin (Quay et al., 1992; Melack & Forsberg 2001; Engle et al., 2008; 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 over-representation of recent floodplain CO_2 flux estimates (e.g., Rasera 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 CO_2 fluxes as well as fluxes from soil when these forests are not inundated.

Abril & 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 & 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 CO_2 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 CO_2 fluxes values observed in sheltered flooded forests versus wind exposed forests should be considered in the integration of CO_2 fluxes in forested wetlands.

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Figures

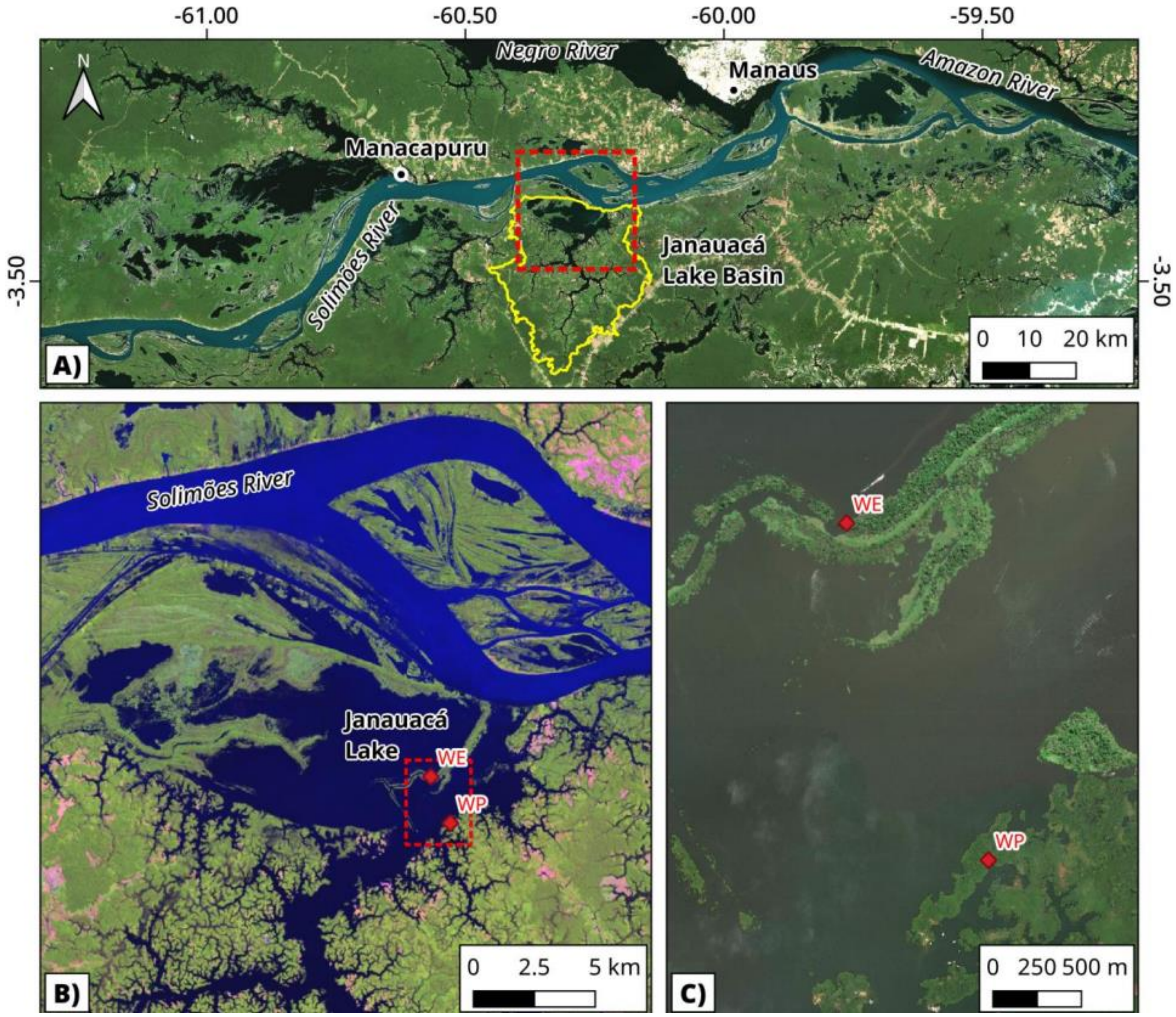

Figure 1. A) General location of the study site showing the watershed (yellow line) (Background: ESRI World Imagery). B) Composite high-water Landsat 8 image showing the upper Janauacá floodplain (red dashed) (R5,G4,B3). C) Location of the sampled flooded forest sites: wind exposed site (WE) and wind protected site (WP). Red dashed lines indicate the boundaries of the following figure panel. Janauacá lake basin delimited by Pinel et al. (2015).

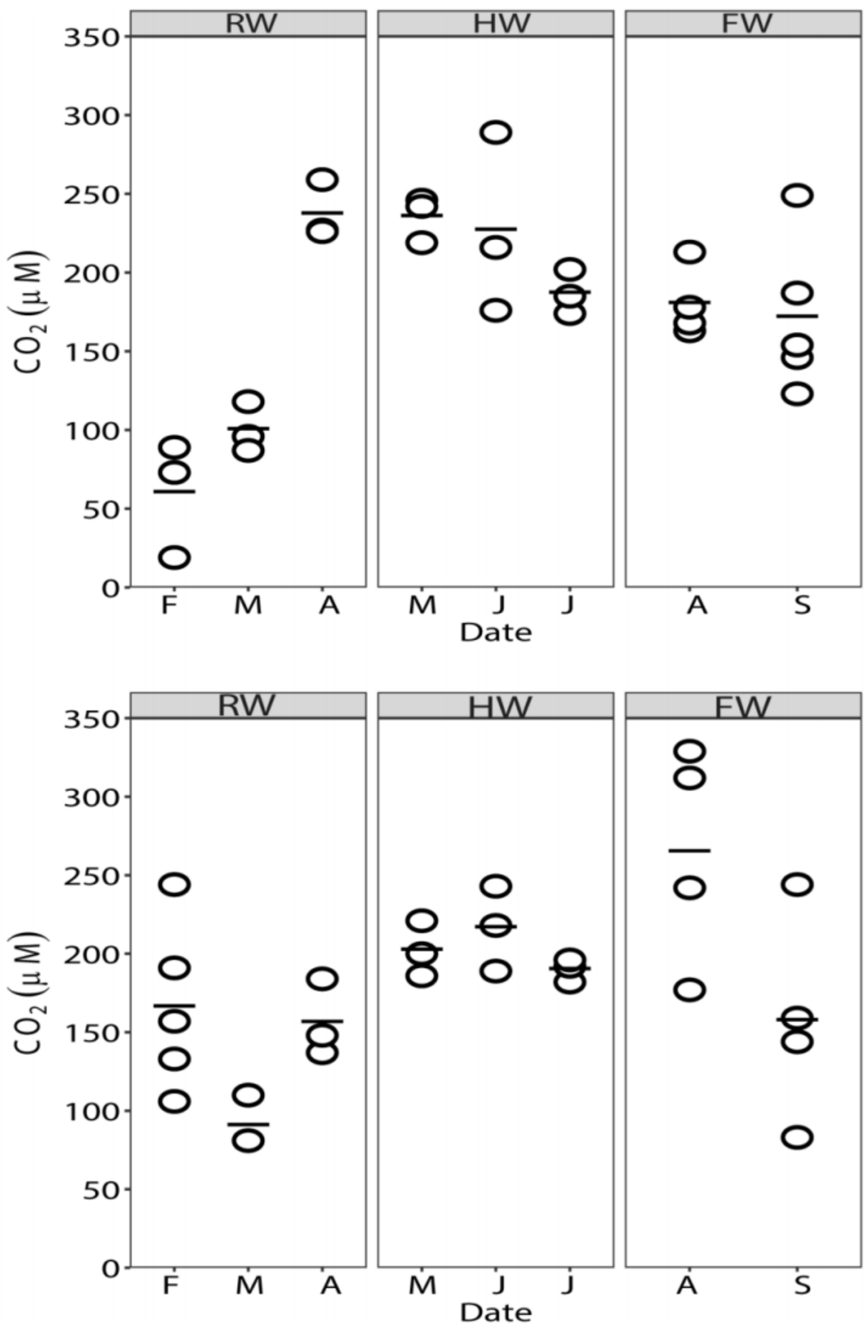

Figure 2. CO_2 concentrations measured at the wind exposed site (WE, upper panel) and wind protected site (WP, lower panel) during the study and divided into hydrological periods: rising water (RW), high water (HW) and falling water (FW). Horizontal bars represent the mean per sampling date, open circles represent each observation in a 24 h period.

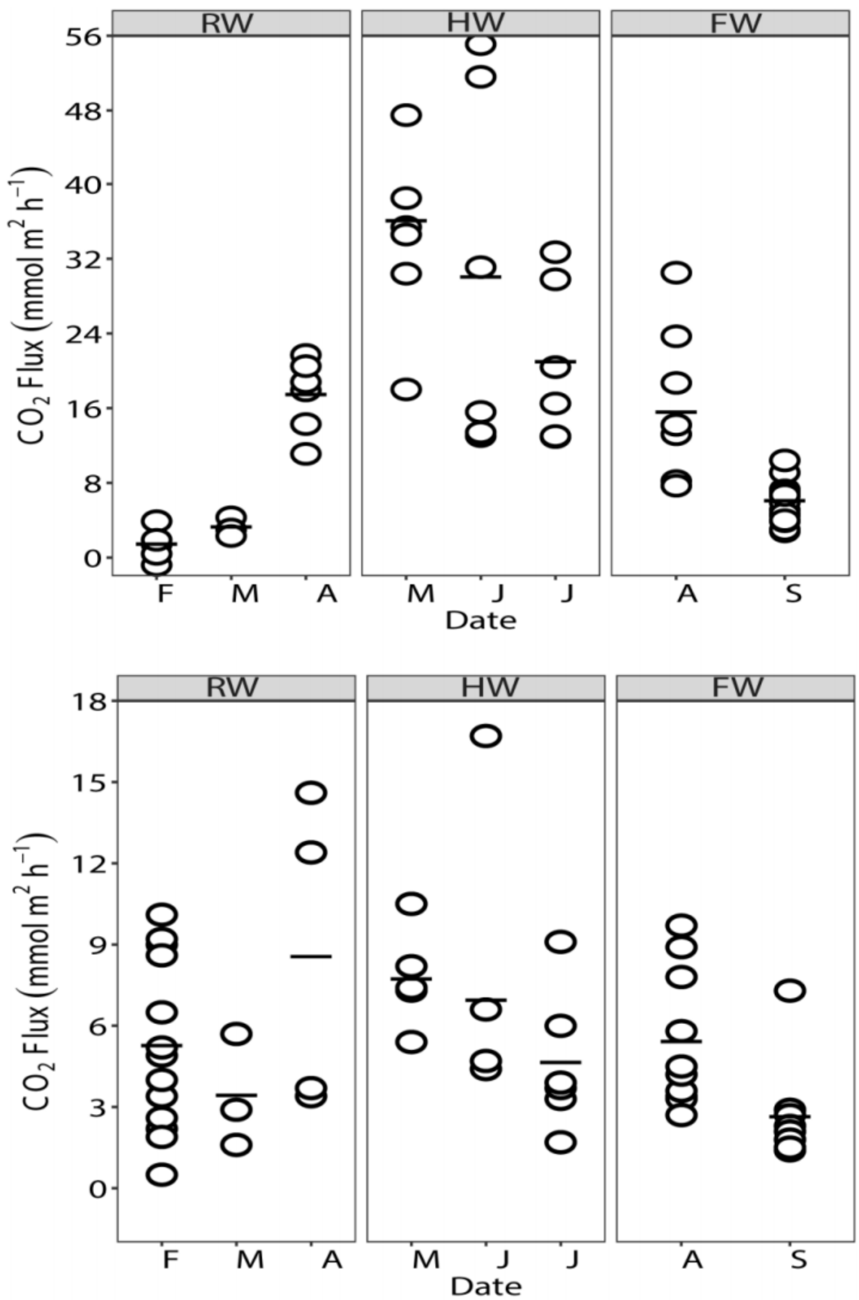

Figure 3. CO_2 evasion measured at the wind exposed site (WE, upper panel) and wind protected site (WP, lower panel) during the study and divided by hydrological period: rising water (RW), high water (HW) and falling water (FW). Horizontal bars represent the mean, open circles represent each observation in a 24 h period. Note differences in scale of y axis between sites.

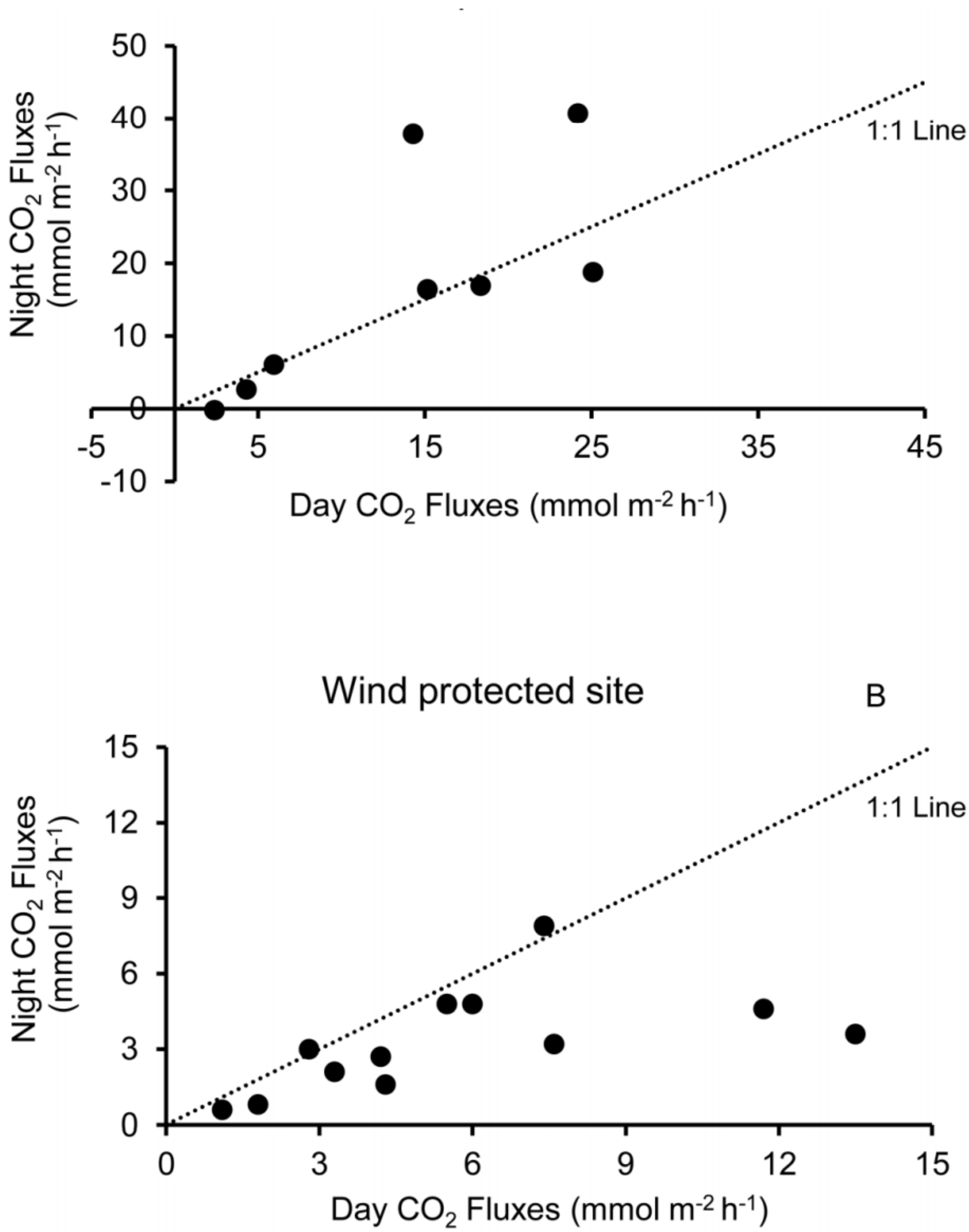

Figure 4. Mean CO_2 fluxes measured during the night versus measurements made during the day for the wind exposed (A) and protected (B) sites. Dashed lines represent the 1:1 equivalence

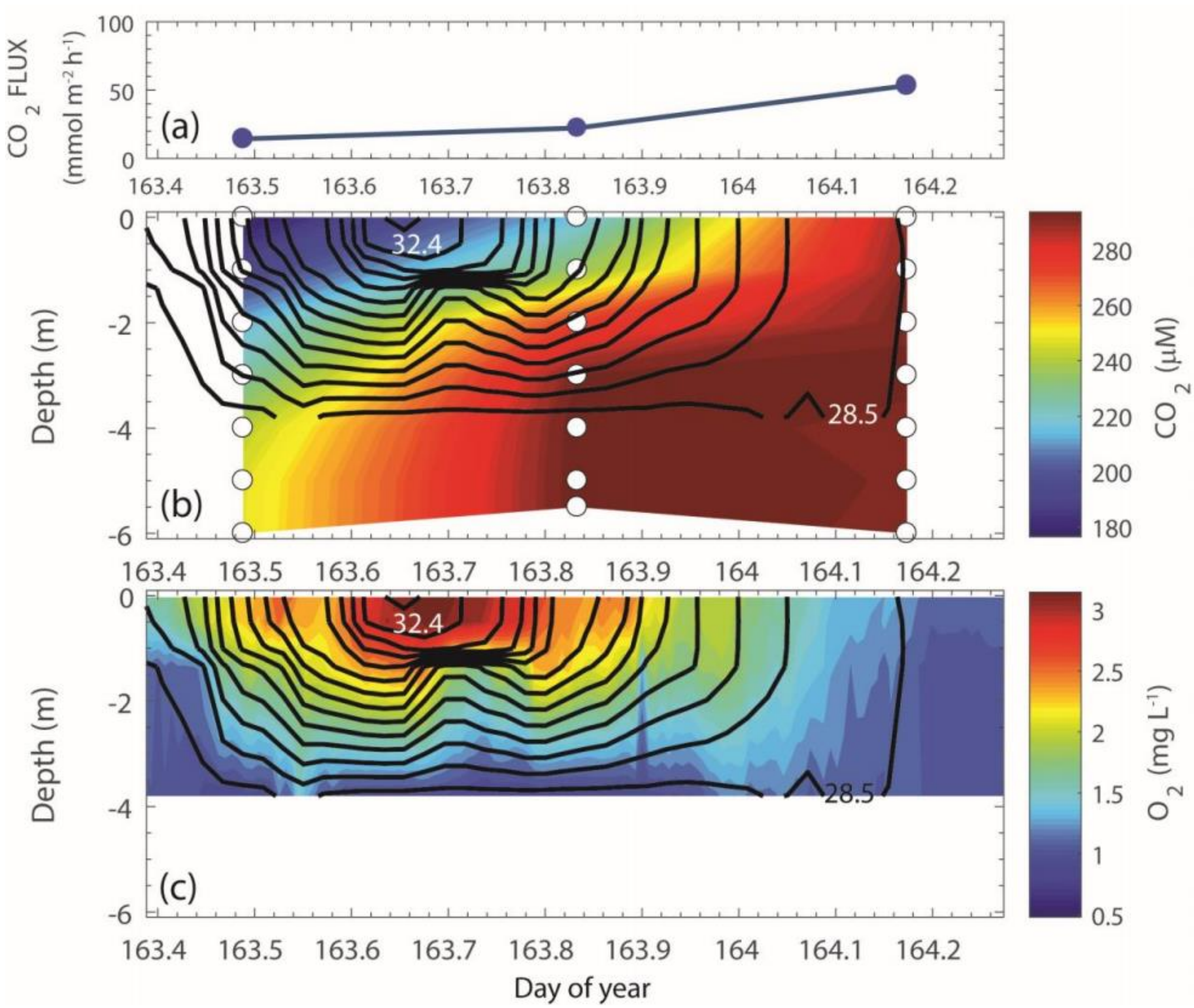

Figure 5. Upper panel) Time series of CO_2 fluxes, Middle panel) Dissolved CO_2 concentrations from discrete measurements at depths indicated by white dots, and Lower Panel) 10 min averaged time series of dissolved oxygen in the wind exposed flooded forest in June 2015. Hourly averaged isotherms at 0.3°C intervals are shown as black contours with maximum and minimum isotherms labelled.

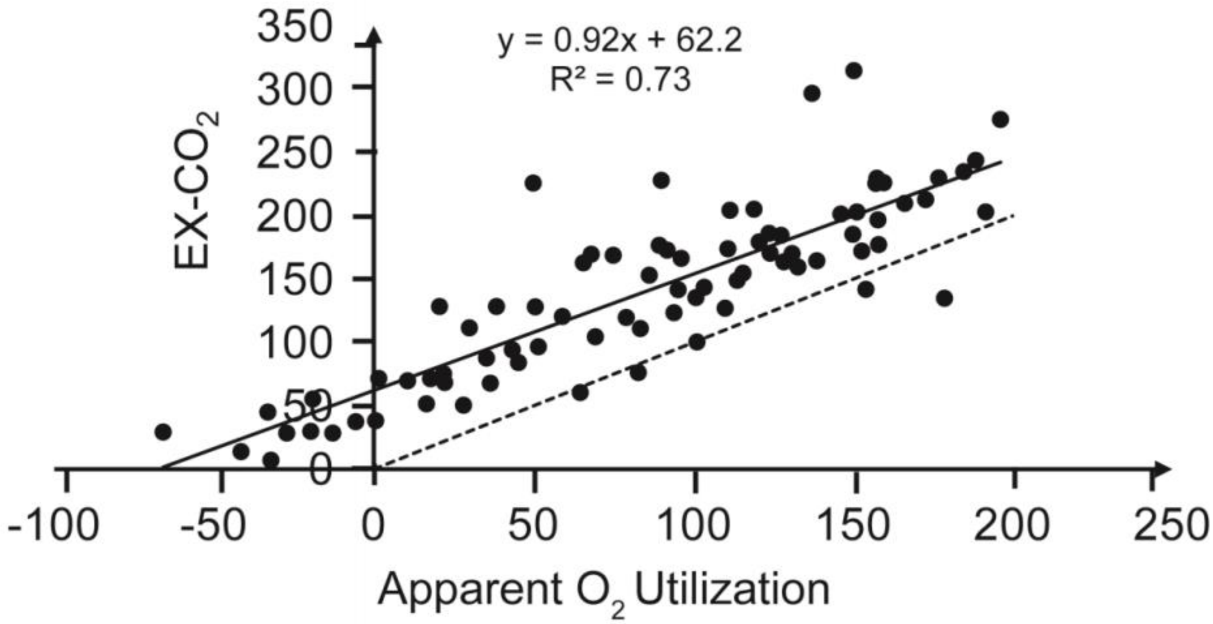

Figure 6. Excess of CO_2 as function of apparent oxygen utilization (AOU) in µM, calculated for the surface waters of inundated forests investigated in our study. Dashed line is the 1:1 line and solid black line is the regression line.

Table 1. Surface CO_2 concentrations, flux and gas transfer velocities (k_{600}) measured in wind exposed (WE) and wind protected (WP) flooded forests. SD is the standard deviation; Min/max indicates the minimum and maximum values among the n measurements on each date.

PERIOD	MONTH	CO_2 (μM)		CO_2 Flux (mmol $m^{-2}h^{-1}$)		K_{600} (cm h^{-1})	
		WP Mean, SD (Min/max, n)	WE Mean, SD (Min/max, n)	WP Mean, SD (Min/max, n)	WE Mean, SD (Min/max, n)	WP Mean, SD (Min/max, n)	WE 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* / 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)
High Water	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)
	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)
Falling Water	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)
	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	July 2016	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)	

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*The in-gassing value was measured under high Chl-*a* concentrations; 18 μgL^{-1} in the flooded forest and $25\ \mu gL^{-1}$ in associated open waters, suggesting that Chl-*a* enriched water was advected from the open waters to the flooded forest site. We had one replicate measurement with negative flux and another with a positive flux, but both with high r^2 (>0.95). When replicates were averaged, the value was still negative.

Table 2. Average CO_2 diffusive fluxes (FCO_2) 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 $\pm$ 599
Georgia, USA[c]	Floodplain	chamber	115 – 1270*
Congo basin[d]	Floodplain	chamber	2640 $\pm$ 1370
Pantanal, Brazil[e]	Floodplain	modeled	320
Northern Australia[f]	Floodplain	chamber	1260 $\pm$ 1258
Amazon basin[g]	Floodplain	chamber	2182 $\pm$ 2954

[a] Devol et al., 1988. Mean value calculated from nine measurements made during the high-water period.

[b] Happell & Chanton,1993. Mean value calculated from single daytime measurements once a month for one year.

[c] Pulliam, 1993. *Range of mean daily fluxes obtained from ten transects with three measurements done at a monthly frequency for a two-year period.

[d] Tathy et al., 1992. Mean value from eleven daily measurements made in flooded forests.

[e] Dalmagro et al., 2018. Mean value obtained using 40 measurements of surface CO_2 water concentrations and a wind-based equation during the flooded season (March to June).

[f] Bass et al., 2014. Mean value obtained from seven sites with daily replicate measurements done eight times during the flood season (February to May).

[g] This 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.