

Gap-filling measurements of carbon dioxide storage in tropical rainforest canopy airspace

Hiroki Iwata^{a,*}, Yadvinder Malhi^{b,c}, Celso von Randow^d

^a *Terrestrial Environment Research Center, University of Tsukuba, Tsukuba 305-8577, Japan*

^b *Oxford University Centre for Environment, University of Oxford, Oxford OX1 3QY, UK*

^c *School of GeoSciences, University of Edinburgh, Edinburgh EH9 3JU, UK*

^d *Alterra, Wageningen University and Research Center, P.O. Box 47, 6700 AA, Wageningen, The Netherlands*

Received 26 October 2004; received in revised form 12 August 2005; accepted 16 August 2005

Abstract

For the determination of biotic fluxes of carbon dioxide (CO₂) or other trace gases to or from a forest canopy, it is important to measure the storage of the trace gas within the forest canopy in addition to the net vertical flux above the forest canopy. However, the data continuity of within-canopy storage measurements can be poor because these measurements are subject to frequent equipment breakdowns. We here explore methods for gap-filling within-canopy CO₂ storage, using the data derived from an Amazonian rainforest (Caxiuanã). Our first approach was to estimate hourly storage from hourly CO₂ concentration measured above the canopy at the tower top. This proved unreliable, since at this hourly time scale the variations in above-canopy CO₂ are often decoupled from local changes in within-canopy storage. We then explored a second approach based on determination of the *total* CO₂ accumulation over a night. This was found to be adequately correlated with a time-weighted friction velocity (u_{*w}) averaged over a night ($R^2 = 0.42$). The total night-time storage was then used to model daytime depletion of CO₂ within the canopy. The gap-filling model was validated against independent data from the same site, and also applied to another tropical forest (Jarú) with similar results. The modelled storage is in good agreement with the measured storage, and by reducing susceptibility to advection error it is in some ways superior to the direct storage measurements. This suggests at the possibility of a general method for estimating storage in forest canopies, with re-calibration for each site.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Within-canopy CO₂ storage; Gap-filling method; Tropical rainforest; Friction velocity; Eddy covariance method

1. Introduction

Over the past decade, there has been a proliferation of studies utilising micrometeorological methods to quantify the flux of carbon dioxide (CO₂) and other trace gases between vegetation canopies and the atmosphere (Baldocchi et al., 2001). Whilst the focus of these studies has been on above-canopy fluxes, there

was an early realisation that there can be significant storage of trace gases within the canopy airspace. The degree of storage varies with the intensity of boundary-layer turbulence and thus over the diurnal cycle. For CO₂ and other trace gases with nocturnal, sub-canopy emissions, there is a tendency of accumulation of the trace gases within the canopy airspace at night, and a depletion of this store in the early morning as thermal convection sets in.

Whilst the net effect of the storage of CO₂ over a full diurnal cycle is approximately zero (night-time accumulation = daytime loss), it can be important to measure this storage if our interest is to estimate the

* Corresponding author. Tel.: +81 29 853 2531;
fax: +81 29 853 2530.

E-mail address: hiroki@suiri.tsukuba.ac.jp (H. Iwata).

Nomenclature

C	CO ₂ concentration ($\mu\text{mol m}^{-3}$)
C_{top}	CO ₂ concentration measured by the eddy covariance instrumentation at the top of the tower ($\mu\text{mol m}^{-3}$)
d	zero-plane displacement (m)
h	the height of eddy covariance instrumentation (m)
LW	above-canopy downward long-wave radiation (W m^{-2})
R^2	coefficient of determination
RMSE	root mean square error
S_c	accumulated storage during night ($\text{g (C) m}^{-2} \text{night}^{-1}$)
S_c/F_{biotic}	ratio of night-time storage to night-time biotic flux
S_c/F_c	ratio of night-time storage to night-time above-canopy flux
T_a	air temperature at tower-top ($^{\circ}\text{C}$)
T_s	soil temperature ($^{\circ}\text{C}$)
u^*	friction velocity at tower-top (m s^{-1})
u^*_{w}	time-weighted friction velocity averaged over a night (ms^{-1})
z	height above the ground surface (m)
$(z - d)/L$	Monin–Obukhov stability parameter (dimensionless)

“biotic” flux of the trace gas, and understand its physiological controls. The biotic flux (or net ecosystem exchange, NEE) is defined as biotic flux = above-canopy flux + storage flux. Measurement of within-canopy storage is now standard in many canopy flux measurement studies, with the most common approach using a gas analyser to measure gas concentrations from a sampling system that automatically cycles between intakes at various heights within the forest canopy. The mechanical nature of these measurements, however, means that there can often be problems of equipment breakdown (e.g. pump failure and solenoid switch failure), especially in challenging environments such as remote tropical forests (with problems with insects and humidity) or boreal forests (with problems with insects and icing). Therefore, the data continuity of storage measurements may often not match those of the above-canopy measurements. A reliable method of “gap-filling” measurements for within-canopy storage would clearly be desirable.

In this paper we explore the potential of various approaches to gap-filling measurements of storage in tropical forest canopies, utilising either data from the

above-canopy flux measurements or from meteorological observations. In addition to describing a technical procedure, this paper is also of more general value in its exploration of the determinants of within-canopy CO₂ storage. We first explore the potential of utilising hourly or 30-min observations of above-canopy turbulence and CO₂ concentration. This approach is demonstrated to be unreliable, because at this time scale the variations in above-canopy CO₂ are often decoupled from local changes in within-canopy storage, and more influenced by advection from nearby regions.

In homogeneous canopies, advection problems are often related to limited sampling times, and we then explore an approach of utilising the mean meteorological or turbulence conditions over the entire night to estimate the total storage over the night. Total night-time storage is found to be more consistently predictable, and we then develop empirical relationships between total storage and the daytime evacuation of CO₂ from the canopy. Our aim here is to present an approach to site-specific gap-filling of CO₂ storage, but we also present evidence that there may be generalities in the storage phenomenon that are consistent across forest sites.

In summary, the questions that we address in this paper are:

- (1) can the accumulation of CO₂ in a forest canopy be predicted from standard turbulence or meteorological variables?
- (2) which variable is the best predictor of CO₂ storage?
- (3) is the relationship between storage and turbulence invariant between forest sites?

2. Methods

2.1. Sites and measurements

The data used in our main analysis were collected in the Caxiuana National Forest ($1^{\circ}43'\text{S}$, $51^{\circ}27'\text{W}$, 20 m above mean sea level), approximately 350 km to the west of the city of Belém, Pará, Brazil. This is an extensive, undisturbed, dense lowland tropical forest with a mean annual rainfall of 2400 mm, a mean canopy height of 35 m, an above-ground dry biomass of 330–430 t ha⁻¹ (Wood et al., submitted for publication) and a leaf area index of 5–6 (P. Meir, unpublished data). Further site details are given in Carswell et al. (2002). The Edisol eddy covariance system (Moncrieff et al., 1997) was mounted above a 51.5 m tall aluminum tower. Eddy covariance sensors were mounted 4 m

above the tower (i.e. at a total height of 55.5 m above-ground level) on the easterly side so as to minimize flow distortion for the prevailing wind direction (which was easterly both day and night). Within- and above-canopy measurements of CO₂ were made at six heights (0.2, 2.0, 8.0, 16.0, 32.0 and 55.5 m), with the topmost intake being the outflow from the eddy covariance system to provide cross-calibration between the two measurement systems. The profile system sampled each height for 5 min, cycling through the entire profile every half hour. At each height, 2 min were allowed for flushing residual air from the tube before measurement using an infrared gas analyser (PP Systems, Hitchin, UK). Vertical profiles of CO₂ concentration were collected in batches as follows: between 16/04/1999 and 11/06/1999, between 24/06/1999 and 08/08/1999, between 06/09/1999 and 09/09/1999 and between 07/10/1999 and 19/10/1999 (most of the time corresponding to dry season), before final mechanical breakdown of the system. The data acquisition percentage during the storage measurement period was approximately 47% and the mean daily storage was 0.32 μmol m⁻² s⁻¹ with skewness of -0.32.

Another site used for comparison was Jarú (10°5'S, 61°56'W, 145 m above mean sea level) which is located about 100 km north of Ji-Paraná, Rondônia, Brazil. This undisturbed tropical forest has the same mean canopy height (35 m) as the Caxiuanã forest and the storage measurement was performed at six heights (0.05, 2.7, 25.0, 35.0, 45.0 and 62.7 m) at the same sampling interval as Caxiuanã (i.e. 5 min intervals). A mean annual rainfall of 1900 mm (Culf et al., 1996), an above-ground dry biomass of 220 t ha⁻¹ and a leaf area index of 4.0 (Meir, 1996) indicate that Jarú forest is drier and less dense than Caxiuanã forest. The storage data used in this paper is between 19/04/1999 and 24/05/1999 (34 days in total), which corresponding to the early dry season. Further details are given in Von Randow et al. (2004).

2.2. Calculation of storage from concentration profiles

For Caxiuanã, within-canopy CO₂ concentrations calculated from the non-synchronous measurements at different heights were interpolated in time to provide instantaneous profiles at half-hour intervals, and these profiles were then interpolated vertically to estimate the total CO₂ stored. A cubic spline scheme was used for both interpolations, but comparison with a linear interpolation demonstrated that the calculated storage

was insensitive to the details of the interpolation method. A similar calculation procedure was applied for Jarú. However, interpolation in time was not performed, and only linear interpolation was performed vertically (Von Randow et al., 2004).

2.3. Estimation of storage from above-canopy concentration measurements

We first tried to estimate within-canopy storage from measurements of the change of CO₂ concentration at the top of the tower, as measured by the eddy covariance instrumentation. Our hypothesis was that the top-of-canopy change in concentration was related to the total storage by an unknown function $f(u_*)$, i.e.

$$\frac{dC_{\text{top}}}{dt}h = f(u_*) \int_0^h \frac{dC}{dz} dz \quad (1)$$

where C_{top} is CO₂ concentration measured on the top of the tower, h the height of eddy covariance instrument, f an unknown function of the friction velocity (u_*), C CO₂ concentration at each height of profile measurement and z is above-ground height. The function f would be expected to range between 0 and 1, and become close to 1 when u_* is high.

2.4. Relation of total night-time storage to environmental conditions

We next tried to evaluate whether the total night-time CO₂ storage was more predictable than 30-min or hourly storage, through a number of linear and logarithmic regressions using night-time averaged variables.

$$S_c = a f(x) + b \quad (2)$$

where S_c is accumulated storage during night, function f can be linear or logarithmic, and a , b are fitting parameters. Night-time was defined as 18:00–06:00 h, and showed little seasonal variation in timing at this equatorial location. For variable x several night-time averaged variables were tested as listed in Table 1. To reflect the fact that turbulent conditions immediately prior to dawn are more relevant in determining dawn concentrations, a time-weighted friction velocity (u_{*w}), which applied a linear weighting that increased with hour of the night, was also tested for variable x , i.e.

$$u_{*w} = \frac{\sum_{n=1}^{12} u_{*n} n}{\sum_{n=1}^{12} n} \quad (3)$$

Table 1

Values of the coefficient of determination, R^2 , derived in the regressions: $S_c = af(x) + b$

	u_*	u_{*w}	T_a	T_s	$(z - d)/L$	LW
Linear	0.29**	0.35**	0.035	0.0006	0.14*	0.23**
Log	0.36**	0.42**	0.035	0.0005	0.18*	0.23**

Linear and logarithmic functions are used for function $f(x)$. Variables in the header row were substituted as the variable x .

* $P < 0.01$.

** $P < 0.001$.

where n is the number of hours since the beginning of night (weighting factor) and u_{*n} represents u_* at n th hour. From the definition of night-time above, $n = 1$ corresponds to the 18:00–19:00 h. The total night-time storage was then used to model the cycle of daytime depletion of the forest canopy by convective motion using a linear equation below,

$$S_{ci} = a_i S_c \quad \text{for } i = 1, 2, 3, \dots, 12 \quad (4)$$

where S_{ci} is hourly daytime storage at i th hour and a_i is the fitted parameter for the i th hour. The subscript i begins at 6:00 h. We assumed that there was no storage change during daytime if no accumulation occurred during the previous night. To model hourly night-time storages we assumed that hourly biotic fluxes did not vary significantly over the course of any one night, and allocated the total storage so that the night-time total fluxes were constant. This could be improved by modelling total fluxes as a function of temperature and moisture—such variations are generally minor at this wet tropical forest site, but would clearly be more important at seasonally dry forests or temperate or boreal forests. Eight days of data were excluded to act as a validation dataset, and the robustness of this model was validated against those data.

3. Results and discussion

3.1. Hourly storage and above-canopy CO_2 measurements

The relationship between CO_2 storage estimated from CO_2 concentration at the top of the tower and measured CO_2 storage is shown in Fig. 1. The data were divided into three ranges of u_* , with the expectation that agreement would be better when u_* is high. The ratio function $f(u_*)$, as defined in Eq. (1), is plotted in Fig. 2. There is no tendency of increasing $f(u_*)$ with increasing u_* , and the scatter in individual data points is so large that this function is of little

descriptive value. Clearly, variations in above-canopy CO_2 concentration do not reflect variations in storage immediately below, i.e. the above-canopy airspace is decoupled from the within-canopy airspace immediately below, and both terms could be strongly influenced by advection. This decoupling could be enhanced by the fact that the measurement height is 20 m above the 35 m forest canopy. Hence, at tropical forest sites at least, the prospect of directly deriving storage from above-canopy concentrations is poor. The estimated CO_2 storage from the top of the tower were aggregated to derive total night-time storage and compared with corresponding measured storage (Fig. 1d). However, the scatter is large when averaged night-time u_* is low, thus making the use of CO_2 concentration at the top of the tower for gap-filling inappropriate.

3.2. Total night-time storage and mean meteorological and turbulence conditions

Problems with advection in and above homogeneous vegetated canopies are often indicative of inadequate sampling times, and the storage flux over longer periods (e.g. the entire night) may be more predictable than hourly storage flux using some mean meteorological or turbulent parameter. The R^2 values of linear and logarithmic fits between total night-time storage (S_c) and a number of parameters (air temperature T_a , soil temperature T_s , Monin–Obukhov stability parameter $(z - d)/L$, downward longwave radiation (LW, an indicator of nocturnal cloudiness), friction velocity u_* and time-weighted friction velocity u_{*w}) are shown in Table 1. Time-weighted friction velocity u_{*w} is defined in Eq. (3). A logarithmic regression against u_{*w} was the best predictor of total night-time storage, explaining 46% of the total variance. Logarithmic regressions performed better than linear regressions. T_a , T_s , $(z - d)/L$ and LW were of little predictive value with either linear or logarithmic and did not show any improvement when logarithmic regression was used. Therefore, only u_* and u_{*w} were considered further. This result seems to be reasonable since the exchange processes at the atmosphere-canopy interface during night-time (when there is no thermal convection generated by solar heating) are strongly dominated by sweep-ejection cycles (e.g. Baldocchi and Meyers, 1988), and thereby effect of turbulence (i.e. u_*) on night-time accumulation is more important than that of T_a , T_s , $(z - d)/L$ and LW. The disadvantage of using direct regressions to predict change in total storage was that this did not allow for any variation in total respiratory efflux over the

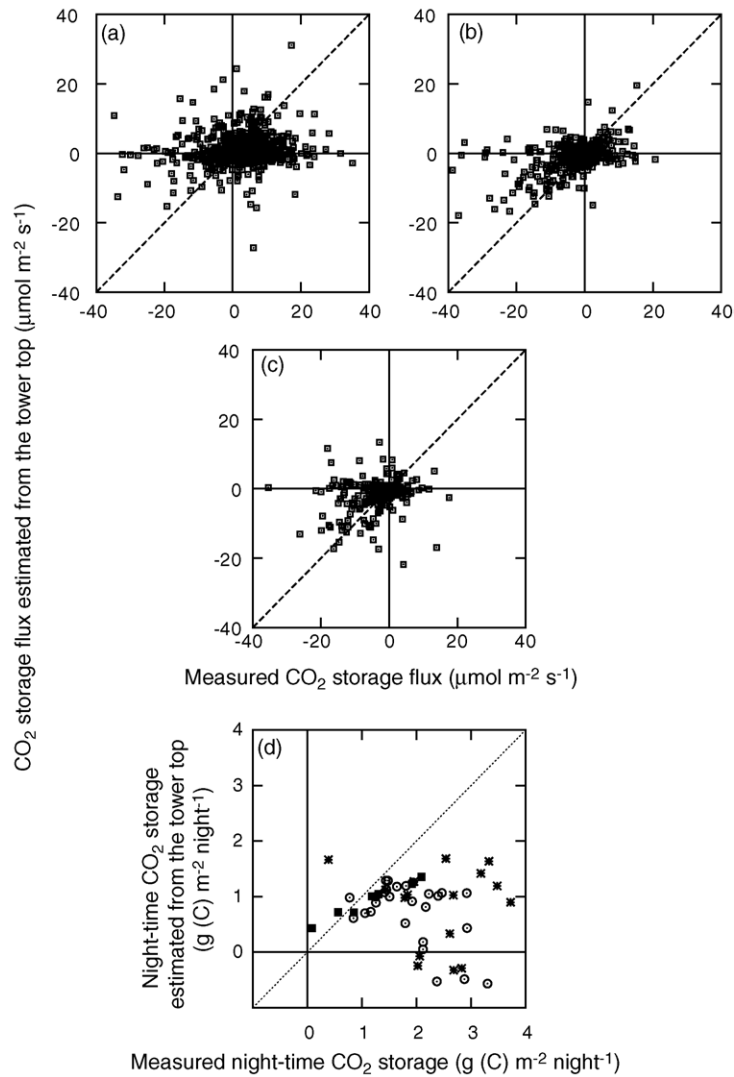


Fig. 1. The comparisons between measured CO₂ storage from profile measurements (x-axis) and CO₂ storage estimated from the tower top (y-axis). The data were separated according to u_* classes: (a) $u_* < 0.2 \text{ m s}^{-1}$, (b) $0.2 \text{ m s}^{-1} < u_* < 0.4 \text{ m s}^{-1}$, (c) $0.4 \text{ m s}^{-1} < u_*$ and (d) the similar comparison for total night-time CO₂ storage for different ranges of averaged night-time u_* : $u_* < 0.1 \text{ m s}^{-1}$ (asterisks), $0.1 < u_* < 0.2 \text{ m s}^{-1}$ (open circles), $0.2 \text{ m s}^{-1} < u_*$ (solid squares).

measurement period. It would be more appropriate to predict the storage fraction of total efflux (S_c/F_{biotic}) or the ratio of storage to above-canopy flux (S_c/F_c). These ratio factors purely describe the relative ratio of storage change to above-canopy flux, and thus describe the canopy physics independent of the biotic flux of CO₂ into the canopy space. Logarithmic regressions with these variables instead of absolute storage show a moderate improvement of fit, explaining at maximum 58% of the total variance (Table 2). However, these variables do present a practical problem in calm conditions when the above-canopy flux is close to zero:

when F_c is close to zero small errors in the measurement of F_c become important and can lead to large errors in the estimate of total biotic flux. The ratio approach was not found to be numerically robust. Hence, the approach of logarithmic regression of absolute storage against u_{*w} was chosen as the most appropriate model. The relationship is shown in Fig. 3. For sites with significant seasonal variations in environmental parameters, the values of a and b may need to be adjusted for each month or season. However, because of the limited time-span of the data set used in this analysis, only one set of values of a and b was used.

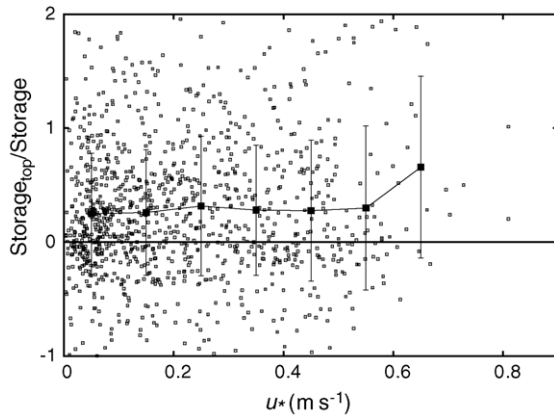


Fig. 2. The ratio of storage estimated from the tower top CO₂ concentration to measured storage. The ratio was averaged in u^* bins of 0.1 m s⁻¹. The error bars show their standard deviation.

3.3. Daytime depletion of stored CO₂

The nature of daytime depletion of canopy CO₂ is shown in Fig. 4a, which shows the mean diurnal CO₂ storage flux during daytime for different values of night-time storage. The peak depletion rate is a function of total stored CO₂, but there is little variation in the shape of the depletion curve. The depletion rate peaks at about 8:30 a.m., and the canopy is always well mixed with the atmosphere by about 13:30 p.m. After this, slight accumulation was observed, which may be caused by increased respiration following temperature increase, combined with possible stable thermal stratification of the lower canopy airspace. Integrating these lines and converting to g (C) m⁻² day⁻¹ yielded total daytime depletions of -1.02, -2.00, -2.74 and -3.55 g (C) m⁻² day⁻¹ for night-time storage range of 0.5–1.5

Table 2

Values of the coefficient of determination, R^2 , derived in the regressions: $y = af(x) + b$, using ratio factors for y , and linear of logarithmic functions for $f(x)$

	u^*	u^*_{w}
Linear		
S_c/F_c	0.30 (8×10^{-4})	0.42 (4×10^{-5})
S_c/F_{biotic}	0.29 (6×10^{-4})	0.35 (1×10^{-4})
S_c	0.29 (3×10^{-5})	0.35 (3×10^{-6})
Log		
S_c/F_c	0.35 (2×10^{-4})	0.56 (4×10^{-7})
S_c/F_{biotic}	0.37 (7×10^{-5})	0.47 (3×10^{-6})
S_c	0.36 (2×10^{-6})	0.42 (1×10^{-7})

The values in brackets are significance values. For comparison, R^2 values using absolute storage, S_c , for y were also included from Table 1.

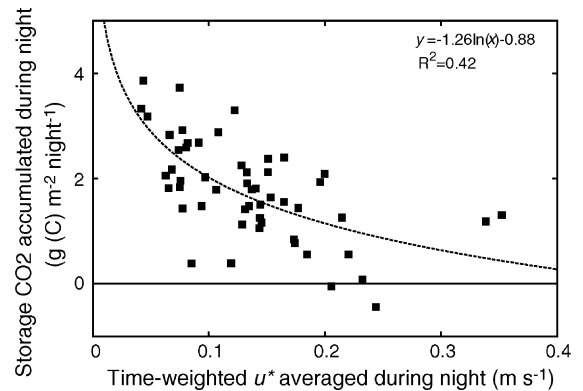


Fig. 3. CO₂ storage accumulated during the night plotted against time-weighted u^* for that night. Night-time was defined as 18:00–06:00 h, the period of zero solar radiation.

(actual average 1.11), 1.5–2.5 (average 1.98), 2.5–3.5 (average 2.86) and 3.5–4.5 (average 3.83) line, respectively. The last storage range contained only five points and is of limited significance: otherwise the storage measurement worked fairly well (daytime depletion = night-time storage). We modelled this depletion curve by regression of the depletion rate at each hour against total storage in the previous night. A linear function defined in Eq. (4) was used for the regression. An example plot is shown in Fig. 5, for time 8:30 a.m. With the exception of a few outliers (probably non-stationary weather events) the depletion flux is approximately linearly proportional to the previous night's storage. The slope of this relationship was calculated for each hour. Fig. 4b shows the mean predicted depletion curves for different values of stored night-time CO₂. As would be expected, the phase and amplitude of the depletion are similar to that in the original data. Integrating these modelled lines and converting to g (C) m⁻² day⁻¹ yielded daytime depletion rate of -0.98, -1.97, -2.95 and -3.94 g (C) m⁻² day⁻¹ for each night-time storage range, respectively, in close agreement with the observed values.

3.4. Model validation against independent data

In order to evaluate the method described above, eight days (18–25 April 1999) of continuously measured storage had been excluded from the model calibration and were now compared with the gap-filled model predictions. The measured and estimated storage CO₂ for the period were compared in Fig. 6a. The model is generally very successful in simulating the diurnal and day-to-day variation in CO₂ storage (RMSE

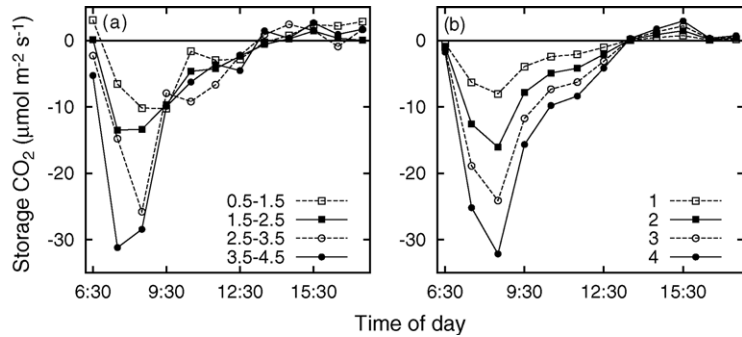


Fig. 4. (a) Actual CO₂ storage cycles averaged according to accumulated storage on the previous night. (b) Modelled daily cycles of CO₂ storage for a given amount of stored CO₂ during the previous night. The key shows the amount of CO₂ stored during the night in units of g (C) m⁻² night⁻¹.

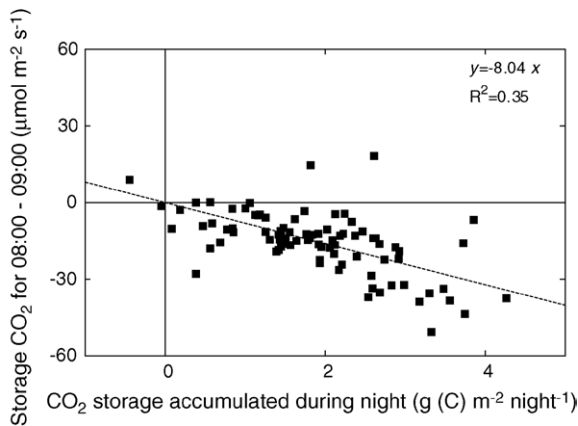


Fig. 5. Regression of storage CO₂ flux over the period 08:00–09:00 h against total night-time accumulation on the previous night.

= 5.87 µmol m⁻² s⁻¹). Both the night-time accumulation and daytime dispersion are well-simulated. The model does not capture extreme peaks in the storage flux. However, as the storage measurement is dependent on a single vertical profile of concentration, it is likely that these extreme peaks represent noise generated by very local advection and sampling problems and this noise is the primary source of data-model discrepancy. Hence, the model may represent storage in the flux footprint more reliably than the direct storage measurement. Evidence for this is shown in Fig. 6b, which shows total biotic flux as derived from the data only, and from the storage model. The plot using modelled storage is much smoother, and the peaks in biotic flux in the data-only plot are unlikely to represent real physiological variations in biotic CO₂ flux. Hence, in some ways the model-smoothed storage flux is superior

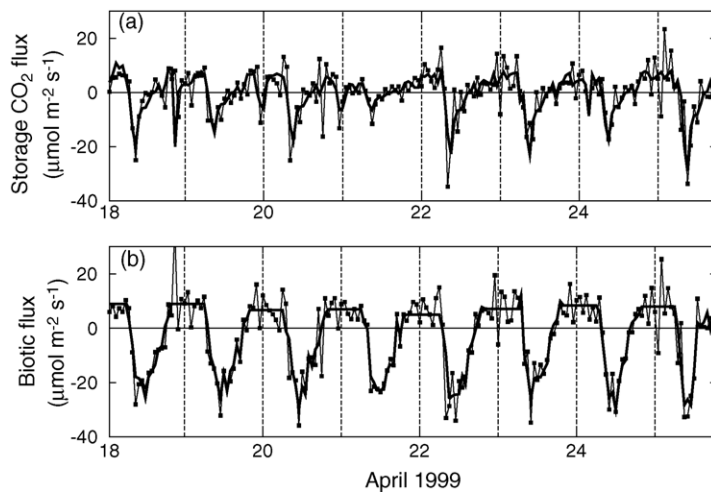


Fig. 6. (a) Measured CO₂ storage (thin solid line with square symbols) compared with estimated CO₂ storage (thick solid line). (b) Measured biotic flux (thin solid line with square symbols) and biotic flux derived from estimated storage (measured above-canopy flux plus estimated storage, thick solid line).

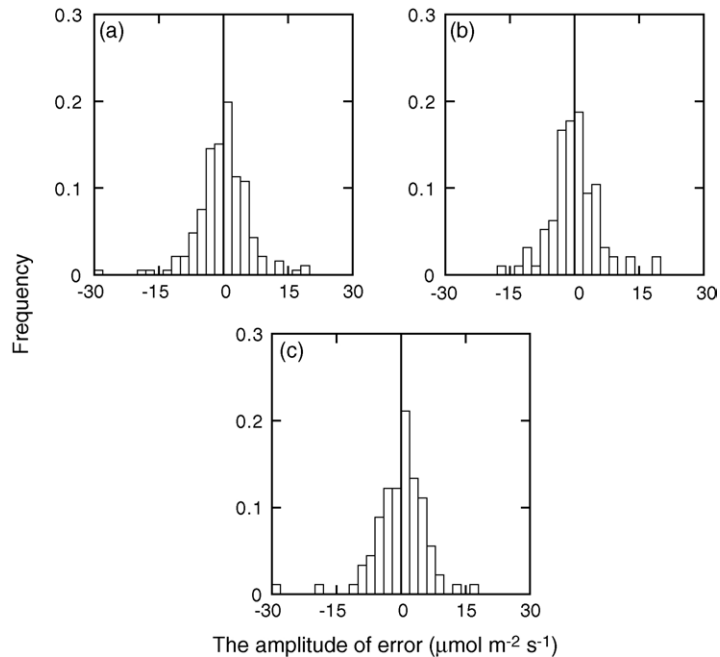


Fig. 7. Histogram of the discrepancy between measured and modelled storage fluxes: (a) all data, (b) daytime data and (c) night-time data.

to the collected storage data. Histograms of the discrepancy between measured and modelled storage fluxes are shown in Fig. 7 and the statistics on the distributions are given in Table 3. There is moderate skewness in the distributions, but this is strongly influenced by the outliers, and the median values are very close to zero, i.e. there is very little evidence of a systematic bias in this approach. As pointed out above, much of the variance in the distributions is more likely to be caused by difficulty in measuring canopy storage in a single profile than by model error.

3.5. Comparison with a second Amazonian forest site

We tested this approach against data from a second Amazonian forest: the Jarú forest in Brazil. The

Table 3

Mean, median, standard deviation, standard error and skewness for the model-data discrepancies shown in Fig. 7

	All ($N = 186$)	Day ($N = 96$)	Night ($N = 90$)
Mean	-0.04	0.057	-0.15
Median	0.10	-0.13	0.51
Standard deviation	5.88	5.76	6.04
Standard error	0.43	0.59	0.64
Skewness	-0.36	0.47	-1.12

The number of data points, N , are indicated in brackets. All units are $\mu\text{mol m}^{-2} \text{s}^{-1}$ (except skewness).

relationship between u_{*w} and accumulated CO_2 storage for Jarú is plotted in Fig. 8 along with the relationship for Caxiuanã. The two relationships are relatively similar, but there is evidence for lower turbulence conditions and higher accumulated storage for a given u_{*w} at Jarú. Several factors influencing on the difference can be ruled out: (1) *seasons*: both data were obtained in dry season. (2) *Biological factors*: the gross primary productivity and leaf area index at Jarú are lower than that at Caxiuanã (Grace et al., 1996; Iwata et al., in preparation). Ecosystem respiration rates are likely to be approximately proportional to productivity, and hence the higher storage at Jarú is unlikely to indicate



Fig. 8. The relationship between u_{*w} and accumulated CO_2 storage for Jarú along with the relationship for Caxiuanã.

higher ecosystem respiration rates. Factors that are likely to contribute to the difference include: (1) *measurement heights of CO₂ profile*: especially, the lowest profile measurement in Jarú forest was at 0.05 m above the ground, which may induce the value of higher accumulation in stable nights. The importance of measuring the first couple of meters is also addressed in Gu et al. (2005). (2) *Topography*: the Caxiuanã tower is located close to the watershed in a weakly undulating landscape, the Jarú tower is closer to the centre of a river valley. Hence, the Jarú tower is less exposed to winds (mean night-time u_* at Jarú is 0.11 m s^{-1} , compared to 0.15 m s^{-1} at Caxiuanã) and more likely to accumulate CO₂ associated with drainage in katabatic flows.

4. Conclusions

To evaluate biotic CO₂ exchange between the vegetation and the atmosphere above, it is crucial to include within-canopy CO₂ storage, particularly in tall forests, in calculating biotic flux. We developed a simple method to estimate the within-canopy storage of CO₂. We found that estimating hourly storage from hourly CO₂ concentration at the tower top is unreliable, since at this time scale the variations in above-canopy CO₂ are often decoupled from local changes in within-canopy storage. We then estimated total night-time CO₂ accumulation from meteorological or turbulence data averaged overnight. The time-weighted friction velocity, u_{*w} , was found to be the most reliable to estimate CO₂ accumulation. This enabled development of an empirical storage accumulation and depletion model that worked successfully when compared to independent data from the same site. Application of the model to independent data showed that, in spite of the simplicity of this approach, the modelled storage was in good agreement with the measured storage. Little bias was found in the error histograms.

The approach presented in this paper is primarily intended as a practical method of gap-filling of storage data. However, the general similarity between two forests in topographically distinct sites hints at the possibility of applying a general correction model. Topographic factors are most likely to explain the difference between the two sites. At present, with only two sites analysed, we suggest that site-specific calibration would be necessary.

In this study, night-time accumulation was estimated from one equation, since the lack of data limited the examination of seasonal variations of accumulation model curve. However, applying different equations for

each month or season may be more appropriate. For sites with stronger temporal variations in temperature, a temperature-dependent model for night-time respiration would be required when allocating estimated night-time storage, rather than constant respiration as used here.

Acknowledgements

We would like to thank Antonio Carlos Lola da Costa, Fiona Carswell, Marcia Palheta, Rafael da Costa, João Athaydes and Alan Braga for their roles in the collection of long term data from Caxiuanã, and Patrick Meir and John Grace for their significant contributions to this project. Research at Caxiuanã was funded by the EU Fifth Framework EUSTACH project as part of the Large-Scale Biosphere Atmosphere Programme in Amazonia (LBA). H.I. would like to take this opportunity to thank Eiji Ohtaki and John Moncrieff for giving him a chance to work on this project. Y.M. gratefully acknowledges the support of a Royal Society University Research Fellowship.

References

- Baldocchi, D.D., Meyers, T.P., 1988. Turbulence structure in a deciduous forest. *Boundary-Layer Meteorol.* 43, 345–364.
- Baldocchi, D., Falge, E., Gu, L.H., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X.H., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw U, K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bull. Am. Meteorol. Soc.* 82, 2415–2434.
- Carswell, F.E., Costa, A.L., Palheta, M., Malhi, Y., Meir, P., Costa, J. de P.R., Ruivo, M. de L., Leal, L. do S.M., Costa, J.M.N., Clement, R.J., Grace, J., 2002. Seasonality in CO₂ and H₂O flux at an eastern Amazonian rain forest. *J. Geophysical Res.* 107, 43,1–43,16.
- Culf, A.D., Esteves, J.L., Marques Filho, A.O., da Rocha, H.R., 1996. Radiation, temperature and humidity over forest and pasture in Amazonia. In: Gash, J.H.C., Nobre, C.A., Roberts, J.M., Victoria, R.L. (Eds.), *Amazonian Deforestation and Climate*. John Wiley and Sons, Chichester, pp. 175–192.
- Grace, J., Malhi, Y., Lloyd, J., McIntyre, J., Miranda, A.C., Meir, P., Miranda, H.S., 1996. The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. *Global Change Biol.* 2, 209–218.
- Gu, L., Falge, E.M., Borden, T., Baldocchi, D.D., Black, T.A., Saleska, S.R., Suni, T., Verma, S.B., Vesala, T., Wofsy, S.C., Xu, L., 2005. Objective threshold determination for nighttime eddy flux filtering. *Agric. For. Meteorol.* 128, 179–197.
- Meir, P., 1996. The exchange of carbon dioxide in tropical forest. PhD Thesis. University of Edinburgh.
- Moncrieff, J.B., Massheder, J.M., de Bruin, H., Elbers, J., Friborg, T., Heusinkveld, B., Kabat, P., Scott, S., Soegaard, H., Verhoef, A., 1997. A system to measure surface fluxes of momentum, sensible

- heat, water vapour and carbon dioxide. *J. Hydrol.* 188–189, 589–611.
- Von Randow, C., Manzi, A.O., Kruijt, B., de Oliveira, P.J., Zanchi, F.B., Silva, R.L., Hodnett, M.G., Gash, J.H.C., Elbers, J.A., Waterloo, M.J., Cardoso, F.L., Kabat, P., 2004. Comparative measurements and seasonal variations in energy and carbon exchange over forest and pasture in South West Amazonia. *Theor. Appl. Climatol.* 78, 5–26.
- Wood, D., Malhi, Y., Baker, T.R., Write, J., Phillips, O.L., Cochrane, T., Meir, P., Lloyd, J., Almeida, S., Arroyo, L., Chave, J., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Vargas, P.N., Pitman, N.C.A., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Martinez, R.V., Vinceti, B. The regional variation of above-ground live biomass in old-growth Amazonian forest, *Global Change Biol.*, submitted for publication.