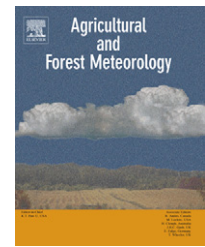


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# Resolving systematic errors in estimates of net ecosystem exchange of CO<sub>2</sub> and ecosystem respiration in a tropical forest biome

Lucy R. Hutyra<sup>a,\*</sup>, J. William Munger<sup>a,b</sup>, Elizabeth Hammond-Pyle<sup>a,b</sup>, Scott R. Saleska<sup>c</sup>, Natalia Restrepo-Coupe<sup>c</sup>, Bruce C. Daube<sup>a,b</sup>, Plinio B. de Camargo<sup>d</sup>, Steven C. Wofsy<sup>a,b</sup>

<sup>a</sup> Department of Earth and Planetary Sciences, Harvard University, Cambridge, MA, USA

<sup>b</sup> School of Engineering and Applied Sciences, Harvard University, Cambridge, MA, USA

<sup>c</sup> Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA

<sup>d</sup> Laboratório de Ecologia Isotópica, CENA/USP, PO Box 96, CEP 13400-970, Piracicaba, SP, Brazil

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## ABSTRACT

The controls on uptake and release of CO<sub>2</sub> by tropical rainforests, and the responses to a changing climate, are major uncertainties in global climate change models. Eddy-covariance measurements potentially provide detailed data on CO<sub>2</sub> exchange and responses to the environment in these forests, but accurate estimates of the net ecosystem exchange of CO<sub>2</sub> (NEE) and ecosystem respiration (R<sub>eco</sub>) require careful analysis of data representativity, treatment of data gaps, and correction for systematic errors. This study uses the comprehensive data from our study site in an old-growth tropical rainforest near Santarem, Brazil, to examine the biases in NEE and R<sub>eco</sub> potentially associated with the two most important sources of systematic error in Eddy-covariance data: lost nighttime flux and missing canopy storage measurements. We present multiple estimates for the net carbon balance and R<sub>eco</sub> at our site, including the conventional “u\* filter”, a detailed bottom-up budget for respiration, estimates by similarity with <sup>222</sup>Rn, and an independent estimate of respiration by extrapolation of daytime Eddy flux data to zero light. Eddy-covariance measurements between 2002 and 2006 showed a mean net ecosystem carbon loss of  $0.25 \pm 0.04 \mu\text{mol m}^{-2} \text{s}^{-1}$ , with a mean respiration rate of  $8.60 \pm 0.11 \mu\text{mol m}^{-2} \text{s}^{-1}$  at our site. We found that lost nocturnal flux can potentially introduce significant bias into these results. We develop robust approaches to correct for these biases, showing that, where appropriate, a site-specific u\* threshold can be used to avoid systematic bias in estimates of carbon exchange. Because of the presence of gaps in the data and the day–night asymmetry between storage and turbulence, inclusion of canopy storage is essential to accurate assessments of NEE. We found that short-term measurements of storage may be adequate to accurately model storage for use in obtaining ecosystem carbon balance, at sites where storage is not routinely measured. The analytical framework utilized in this study can be applied to other Eddy-covariance sites to help correct and validate measurements of the carbon cycle and its components.

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\* Corresponding author. Present address: Department Urban Design & Planning, University of Washington, Seattle, WA 98195, USA. Tel.: +1 206 685 9693.

E-mail address: [lrhutyra@u.washington.edu](mailto:lrhutyra@u.washington.edu) (L.R. Hutyra).

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## 1. Introduction

Tropical rainforests contain large stores of biomass and rapidly cycle carbon through photosynthesis and respiration, giving these ecosystems significant leverage on the global carbon cycle and rate of atmospheric CO<sub>2</sub> increase. Determining the net carbon balance in tropical rainforests is critical for quantifying the global carbon cycle, to understand the component processes of ecosystem respiration ( $R_{\text{eco}}$ ) and photosynthesis, and to define responses of forests to environmental change.

Current research has not adequately constrained the magnitude, or even the sign, of the net carbon balance of tropical rainforests. Plot-level biometric measurements in undisturbed tropical rainforests have observed both significant carbon uptake (Phillips et al., 1998; Baker et al., 2004) and carbon emission (Rice et al., 2004; Miller et al., 2004). Analysis of Eddy-covariance measurements in the Amazon, which integrate carbon exchange over several square kilometers, have similarly observed a range of net ecosystem exchange (NEE) in primary forest sites from net uptake (Grace et al., 1995; Malhi et al., 1998), neutral (Miller et al., 2004), to small net release of carbon to the atmosphere (Hutyra et al., 2007; Saleska et al., 2003). Many modeling studies have predicted net uptake of CO<sub>2</sub> in the wet season and emission in the dry season, driven by temperature and water effects on  $R_{\text{eco}}$  and photosynthesis (respectively), but the opposite seasonality in NEE has been observed at some tropical forests (Saleska et al., 2003). Models predict divergent future scenarios in a changed climate, including collapse of the Amazon forest (Cox et al., 2004) and possible feedbacks between warming, reduced forest cover, and increased aridity (Oyama and Nobre, 2003; Hutyra et al., 2005).

Photosynthesis and its response to primary drivers (temperature and light) are relatively well understood at the leaf level and in environmental chambers (Farquhar and Sharkey, 1982). However, given the very high leaf area and significant variability in vertical and horizontal light interception within tropical ecosystem, it is a significant challenge to scale up leaf level results to the entire forest canopy.  $R_{\text{eco}}$  is a less understood process in tropical forests, integrating both aboveground and belowground plant and microbial processes, each driven by different ecosystem processes and responding differently to environmental drivers (Davidson et al., 2006; Trumbore, 2006).

Measurements from flux towers are a powerful tool for understanding the exchange of CO<sub>2</sub> between the atmosphere and biosphere at the ecosystem scale. The Eddy-covariance technique has been particularly useful for making direct, long-term measurements of CO<sub>2</sub> exchange in forests (e.g. Wofsy et al., 1993; Urbanski et al., 2007). Observed NEE (the sum of Eddy-covariance flux and changes in canopy CO<sub>2</sub> storage) represents the small residual difference between carbon uptake by photosynthesis and carbon loss through respiration.

During the daytime hours, NEE measures the combination of photosynthesis and autotrophic (roots, stem, leaves) and heterotrophic (microorganisms) respiration. In the nighttime, NEE represents  $R_{\text{eco}}$  because photosynthesis is zero. However, calm and stable atmospheric conditions complicate the

interpretation of nighttime fluxes, with potentially significant effects on the computed ecosystem carbon budget (Papale et al., 2006; Falge et al., 2001). Eddy-covariance methods fail to measure NEE when turbulence is absent. Canopy storage, the change in average concentration below the Eddy sensor, in principle should account for respiratory CO<sub>2</sub> that is not transported from the canopy by turbulent exchange, but in practice, some CO<sub>2</sub> flux is 'lost' from the system by transport processes that cannot be measured at a single point (e.g. Staebler and Fitzjarrald, 2004; Aubinet et al., 2002). Considerable prior work has been done to understand and quantify the consequences of periods of low nighttime turbulence and storage measurements. Many investigators have concluded that not correcting for low nighttime turbulence can constitute a selective, systematic error, which can result in an overestimate of carbon sequestration (Goulden et al., 2006; Miller et al., 2004; Aubinet et al., 2002; Moncrieff et al., 1996; Goulden et al., 1996). Not correctly accounting for nighttime storage can also result in a double counting of fluxes (Papale et al., 2006; Gu et al., 2005; Aubinet et al., 2002; Falge et al., 2001). The importance of advection and storage processes are related to instrumentation, site characteristics (heterogeneity, topography, canopy conditions, etc.) and meteorology (Massman and Lee, 2002).

Data gaps exist in all Eddy-covariance data sets; average data coverage has been reported to be only 65% (Falge et al., 2001). Canopy storage measurements are unavailable for long time periods at many flux towers in the Amazon because of the remote locations, challenging environmental conditions, and sustained instrument failures (Iwata et al., 2005), making the assessment of NEE in Amazonian rainforests particularly challenging and error prone. Numerous efforts to standardize methods and protocols of data processing and gap filling have been undertaken (e.g. Papale et al., 2006; Gu et al., 2005; Falge et al., 2001), but local differences in site characteristics, meteorology, and instrumentation have made it difficult to apply them uniformly across the hundreds of flux sites currently in operation. Estimates of integrated annual carbon balance may vary by several Mg C ha<sup>-1</sup> year<sup>-1</sup> depending on the treatment of flux measurements made under calm conditions (Miller et al., 2004; Papale et al., 2006). The consequent carbon-balance problem is particularly significant in the tropics, because the  $R_{\text{eco}}$  fluxes are large throughout the year and constitute a greater fraction of the annual NEE observations, relative to temperate zones.

Biometric data provide another measure of ecosystem carbon dynamics. Repeated measurement of forest structure (biomass, growth, mortality, and recruitment) document changes in aboveground carbon stocks. These data have the potential to elucidate the ecological mechanisms controlling longer term (years to decades) ecosystem carbon balance. Biometric data can also provide an important independent check on flux tower measurements on the time scale of several years (Barford et al., 2001; Curtis et al., 2002; Saleska et al., 2003). Finer scale measurements of respiration (soil, coarse woody debris, etc.) can quantify the efflux rates for different forest components and provide an independent estimate of  $R_{\text{eco}}$ , to check estimates based on Eddy-covariance data (Law et al., 1999; Falge et al., 2001; Chambers et al., 2004).

In this paper we scrutinize 4 years of high quality Eddy-covariance and ground-based measurements in order to constrain measurements of NEE and  $R_{\text{eco}}$  at a Central Amazonian forest site. We demonstrate that not all methods of calculating NEE and  $R_{\text{eco}}$  from flux data are equally plausible by using independent validation methods with meticulous error analyses. Detailed bottom-up budgets for both  $R_{\text{eco}}$  and for net forest carbon balance are presented using repeated measurements and multiple datasets. We discuss the biases associated with lost nighttime flux and missing storage measurements that need to be considered at all flux tower sites. Finally, we propose a robust correction method for determining carbon balance in the absence of storage data and outline a validation framework for Eddy-covariance results.

## 2. Methods

### 2.1. Site description

This study was part of the Brazilian-led Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA-ECO). Measurements were made at sites in the Tapajós National Forest (TNF) near km 67 (TNF<sub>67</sub>; 2°51'S, 54°58'W, Pará, Brazil) and km 83 (TNF<sub>83</sub>; 3.01°S, 54.58°W; Miller et al., 2004) of the Santarém-Cuiabá highway (BR-163). The discussion in this paper is centered on measurements at the TNF<sub>67</sub> site, with model evaluation at the TNF<sub>83</sub> site. The area is largely contiguous, evergreen tropical rainforest extending for tens of kilometers to the north and south, ~6 km west of the BR-163 highway and ~6 km east of the Tapajós River. The forest is on flat terrain and has a closed canopy with a mean height of ~40 m. This forest can be classified as 'old-growth' with abundant large logs, numerous epiphytes, an uneven age distribution, and emergent trees (Clark, 1996). The area averages a 5-month dry season, extending from approximately July 15 to December 15. Additional local site information for the TNF<sub>67</sub> is provided in Hutyra (2007) and Rice et al. (2004). Pyle et al. (submitted for publication) extended the biometric analyses to assess the representivity of the TNF and evaluate regional carbon balances across the TNF (~600,000 ha) and the Manaus, Brazil areas (~100,000 ha).

### 2.2. Ground-based measurements

Ground-based biomass inventories directly measure above-ground carbon stocks. At the TNF<sub>67</sub>, the net aboveground carbon balance can therefore be determined through repeated surveys at four permanent 50 m × 1000 m biometry transects that were established in 1999 adjacent to the Eddy-covariance tower along prevailing wind directions (within the fetch of the tower). All live trees ≥35 cm dbh (diameter at breast height) were surveyed across 19.75 ha and trees ≥10 cm dbh were surveyed across 4.99 ha (a 10 m swath within four 1 km linear transects) in 1999, 2001, and 2005. Estimates of aboveground, whole tree biomass were calculated based on diameter measurements using the allometric relationships reported in Chambers et al. (2001a). Annual tree mortality ( $M$ ) and recruitment rates were estimated through multiple surveys (Rice et al., 2004).

Coarse woody debris stocks (DS) were surveyed using plot-based methods at the TNF<sub>67</sub> site in 2001 (Rice et al., 2004) and partially resurveyed in 2006. Respiration from coarse woody debris ( $R_{\text{CWD}}$ ) was estimated based on first-order kinetics:

$$R_{\text{CWD}} = \bar{k} \times \text{DS}. \quad (1)$$

An unbiased estimate of the mean decay constant ( $\bar{k}$ ), assuming a normal distribution, was approximated by

$$\bar{k} = \exp(-4.117\rho + 0.5 \times [0.62\rho]^2) \quad (2)$$

where  $\rho$  ( $\text{g cm}^{-3}$ ) is the wood density (derived by Chambers et al., 2001b and applied to the TNF<sub>67</sub> in Rice et al., 2004). Based on local measurements by Keller et al. (2004), a mean coarse woody debris (CWD) wood density of  $0.52 \text{ g cm}^{-3}$  and a decay constant of  $0.124 \text{ year}^{-1}$  were used for respiration estimates. We modeled changes in DS and respiration from 2001 to 2006 by accounting for additional inputs ( $M$ ) and losses such that

$$\text{DS}_i = \text{DS}_{i-1} + M - R_{\text{CWD}}. \quad (3)$$

The distribution of CWD density and the mean mortality rates between 2001 and 2006 were assumed unchanged from the complete CWD survey in 2001 and the vegetation surveys in 2001 and 2005, respectively. Error estimates for the modeled CWD stock and respiration rates were obtained using bootstrap analysis (Efron and Tibshirani, 1997). Complete descriptions of our biometric measurement methods, plot design, and early results are provided in Rice et al. (2004) and in a forthcoming paper by Pyle et al. (submitted for publication).

Soil  $\text{CO}_2$  fluxes were measured at the TNF<sub>67</sub> tower site using dynamic, open chambers from 18 March 2001 to 18 September 2004 (Keller et al., 2005). An integrated flow system allowed air to enter the chamber with minimal contact with outside air and minimal pressure fluctuations. The chamber fluxes were calculated from the linear increase of concentration versus time adjusted for the ratio of chamber volume to area and the air density within the chamber. A full description of soil respiration measurement protocols is given in Keller et al. (2005).

Stem respiration data were obtained from Nepstad et al. (2002) based on measurements at the control plot of the 'Seca Floresta' experiment located ~5 km from TNF<sub>67</sub> tower site at 2°54'S, 54°57'W. Stem respiration measurements were made on twenty individual trees in February, April, July, and October of 2004. Based on the relationship between tree diameter and total tree stem surface area reported in Chambers et al. (2004) and plot-based measurements of basal area at the TNF<sub>67</sub>, the stem respiration measurements were converted from  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  relative to stem area ( $F_s$ ) to  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  relative to ground area ( $F_g$ ) as follows:

$$F_g = F_s \text{ TSB} \frac{\text{BA}}{A} \quad (4)$$

where the mean tree stems per tree basal area (TSB) was  $1.55 \text{ m}^2 \text{ m}^{-2}$  (based on relationships reported in Chambers

et al., 2004), and the overall mean basal area (BA) was 110 m<sup>2</sup> over a sample area (A) of 49,900 m<sup>2</sup>.

Martens et al. (2004) made continuous measurements of Radon-222 (<sup>222</sup>Rn) in the forest canopy air and biweekly, campaign measurements of the <sup>222</sup>Rn soil flux at the TNF<sub>67</sub> tower site. <sup>222</sup>Rn is a naturally occurring, inert, radioactive, noble gas, which is emitted almost exclusively from the soil, and its only sink is radioactive decay. <sup>222</sup>Rn measurements methods can be applied during calm, nighttime hours when errors in Eddy-covariance measurements can be high and have been shown to provide reliable gas exchange rates between soils, the forest canopy, and the free atmosphere above (Trumbore et al., 1990; Martens et al., 1992). <sup>222</sup>Rn-derived gas exchange coefficients are merged with CO<sub>2</sub> concentration profile observations to derive estimates of CO<sub>2</sub> emission rates. Martens et al. (2004) reported measurements from the 2001 wet (June–July) to dry (November–December) seasons.

### 2.3. Tower-based measurements

We used the Eddy-covariance method to measure the CO<sub>2</sub> exchange between the forest and the atmosphere from January 2002 to January 2006 at the TNF<sub>67</sub> site. NEE was calculated every hour as the sum of turbulent flux of CO<sub>2</sub> at 57.8 m and the change in canopy CO<sub>2</sub> storage in the column below (Wofsy et al., 1993). A three-axis sonic anemometer (CSAT-3, Campbell Scientific, Logan, UT) and a closed-path infrared gas analyzer (IRGA, LI-6262, Licor, Lincoln, NE) were used to measure the turbulent flux of CO<sub>2</sub> with a sample rate of 8 Hz. A profile system measured canopy concentration of CO<sub>2</sub> at eight levels throughout the canopy in sequence (2 min at each level). The profile measurements were used to estimate the change in the column average CO<sub>2</sub> mass between the ground and flux measurement height and to calculate the column average rate of change of CO<sub>2</sub> storage. The profile system was zeroed between each sequence. Calibrations of the Eddy and profile systems were made every 6–12 h using CO<sub>2</sub> gas standards at 325, 400, and 475 ppm. An additional CO<sub>2</sub> surveillance standard at 380.45 ppm (traceable to NOAA/CMDL) was used once per week throughout the duration of the experiment to ensure the long-term accuracy of measurements. Full descriptions of the instrumentation, experimental design, data processing, and calibrations are given by Hutyra et al. (2007) and Hutyra (2007).

Hutyra et al. (2007) discusses the ‘lost flux’ at the TNF<sub>67</sub> site under calm, nighttime conditions—approximately 57% of the nighttime hours were classified as calm ( $u^* < 0.22 \text{ m s}^{-1}$ ). Between 2002 and 2006, CO<sub>2</sub> flux data were recorded for 81.2% of possible hours with 48.3% of possible hours being turbulent ( $u^* > 0.22 \text{ m s}^{-1}$ ). We corrected for lost nighttime flux by filtering calm hours and replacing the data with the mean value for proximate, well-mixed time periods. The 4-year dataset was divided in sample bins each containing 50 h of well-mixed nighttime observations (median bin size was 12 nights) and a 5% trimmed mean was calculated for each bin. Gap filling for the R<sub>eco</sub> data was based on the mean nocturnal NEE within these short, sub-seasonal intervals. Hutyra et al. (2007) described the full details of the filling algorithms for R<sub>eco</sub> and NEE. The ‘best estimates’ of mean NEE and R<sub>eco</sub> were

obtained from the data during well-mixed periods. The 95% confidence intervals for the flux measurements were calculated by bootstrapping the error distributions during similar (e.g. season, hour and PAR level) time periods (Richardson and Hollinger, 2005). Unless noted otherwise, all parenthetically reported errors are 95% confidence intervals.

Note that, since the vertical coordinate for wind velocities is positive upward, positive values for fluxes denote emission and negative values denote uptake. In the case of canopy CO<sub>2</sub> storage, positive values indicate accumulation while negative values denote venting, thus NEE = flux + canopy storage.

The intercept value,  $a_1$ , of a hyperbolic light response model:

$$NEE = a_1 + \frac{a_2 PAR}{a_3 + PAR}, \quad (5)$$

was used as an independent method to estimate R<sub>eco</sub>. Only daytime hourly data ( $PAR \geq 40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) were used to define the NEE–light relationship and no data filtering based on turbulence was applied.

### 2.4. Canopy CO<sub>2</sub> storage models

We tested two separate empirical models for canopy CO<sub>2</sub> storage which might be used when direct measurements were unavailable. The first model was a simple diel storage model,  $S_{d,i}$ , based on the observed, mean hourly storage values from 4 years of profile storage measurements,

$$S_{d,i} = \bar{S}_i \text{ for } i = 1, 2, 3, \dots, 24 \quad (6)$$

where  $\bar{S}_i$  is the mean measured storage at the  $i$ th hour.

The second storage model was proposed by Iwata et al. (2005) who estimated the total nighttime (20:00–06:00 local time) storage accumulation,  $S_c$ , from

$$S_c = a_1 + a_2 u^*_{*w} \quad (7)$$

where  $u^*_{*w}$  is a time-weighted friction velocity, with

$$u^*_{*n} = \sqrt{-w'u'}, \quad (8)$$

$$u^*_{*w} = \frac{\sum_{n=1}^{12} u^*_{*n} n}{\sum_{n=1}^{12} n}, \quad (9)$$

and  $a_1$  and  $a_2$  are empirical coefficients derived from periods when storage values were recorded, and  $n$  is the number of hours since the beginning of the night. From this definition of night,  $n = 1$  corresponds to 1800–1900 (local time). The  $u^*_{*w}$  estimate weights the dawn condition more heavily than the previous evening. Under the Iwata et al. (2005) formulation, daytime hourly storage,  $S_{c,i}$ , was then estimated using a linear model:

$$S_{c,i} = a_i S_c; \text{ for } i = 1, 2, 3, \dots, 12 \quad (10)$$

where  $S_{c,i}$  is the hourly daytime storage at the  $i$ th hour ( $i = 1$  corresponds to 0600–0700 local time),  $a_i$  is an hourly fitted parameter, and  $S_c$  is the modeled total CO<sub>2</sub> accumulation from

the preceding night (Eq. (7)). The  $S_{c,i}$  and  $S_{d,i}$  are unique estimates of the daytime storage. We denote the combination of the  $S_c$  and  $S_{c,i}$  models as  $S_I$ . We forced both the  $S_I$  and the  $S_d$  models to have a zero mean storage over 5-day intervals to maintain physical realism, although this feature was apparently not included in the original formulation introduced by Iwata et al. (2005). This paper evaluates the storage model proposed by Iwata et al. (2005),  $S_I$ , largely as originally formulated and also examines the simpler diel storage model,  $S_d$ , as an alternative option for correcting for missing storage measurements.

### 3. Results and discussion

#### 3.1. Ground-based measurements

##### 3.1.1. Respiration

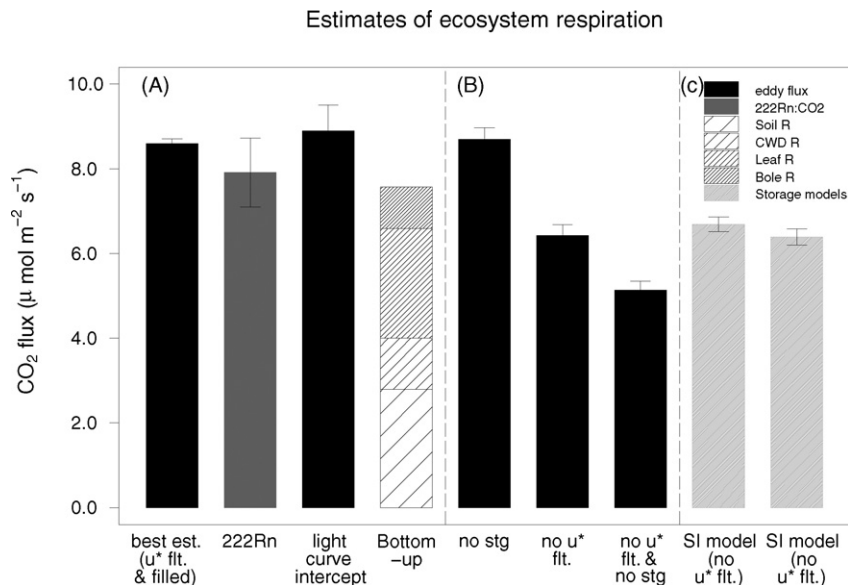
The major components of  $R_{eco}$  include soil (litter, root, and microbial), stem, CWD, and leaf respiration. A bottom-up budget of total  $R_{eco}$ , based on measurements between 2000 and 2006, is shown in Fig. 1, panel A (additional discussion of Fig. 1 will follow in Section 3.4).

Soil respiration, measured by Keller et al. (2005) at the TNF<sub>67</sub> site for 2 years (2000–2001), averaged  $2.76 \pm 0.06 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The mean stem respiration, measured by Nepstad et al. (2002) in the TNF over 4 months in 2000, averaged  $0.62 \pm 0.08 \mu\text{mol m}_s^{-2} \text{s}^{-1}$  relative to stem area and  $1.0 \pm 0.1 \mu\text{mol m}_g^{-2} \text{s}^{-1}$  relative to ground area. Local measurements of leaf respiration were not available. For budgeting purposes, we used the mean observed leaf respiration value of  $2.59 \mu\text{mol m}_g^{-2} \text{s}^{-1}$  reported by Chambers et al. (2004) from a primary Amazonian forest site

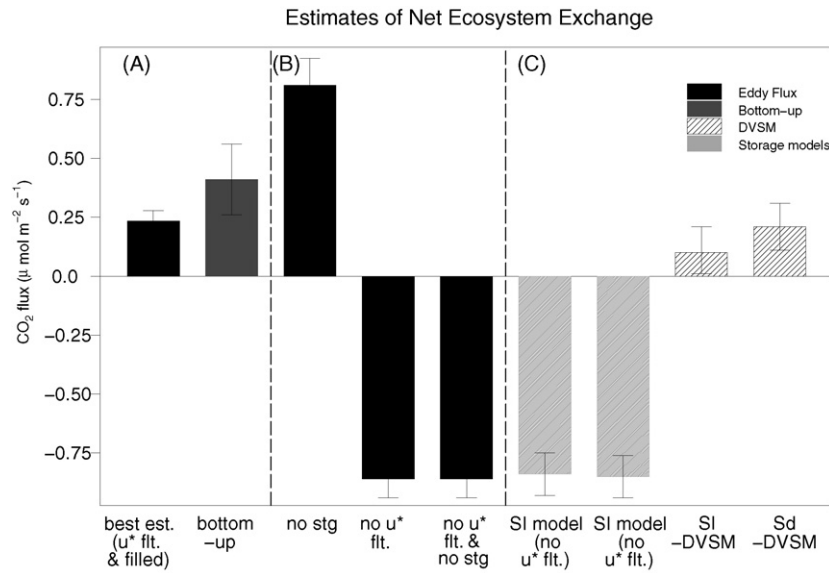
near Manaus, Brazil. No adjustments for possible differences in leaf area index (LAI) were considered since the LAI reported by Chambers et al. (2004) and the observed LAI at TNF<sub>67</sub> are comparable ( $4.7$  and  $4.5 \text{ m}^2 \text{ m}^{-2}$  (Domingues et al., 2005), respectively). Temperature at the Manaus site was also similar in both the diurnal and seasonal patterns to the TNF observations (Malhi et al., 2002; Hutrya et al., 2007).

The mean CWD pool in July of 2001 at the TNF<sub>67</sub> was  $48.0 \pm 5.2 \text{ Mg C ha}^{-1}$  with a mean respiration rate of  $\sim 1.6 \pm 0.3 \mu\text{mol m}_g^2 \text{ s}^{-1}$  (Rice et al., 2004). Additional inputs to the CWD pool were estimated through repeated tree mortality surveys in 2001 and 2005. In the survey intervals of 1999–2001 and 2001–2005 the mean observed mortality was  $2.4 \pm 0.5$  and  $3.0 \pm 0.4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ , respectively. Based on these CWD inputs and the site-specific decay rate constant (Eq. (3)) we estimated a CWD pool of  $37.0 \pm 3.1 \text{ Mg C ha}^{-1}$  in July 2006, representing a  $\sim 23\%$  reduction in stock from the 2001 CWD pool. Based on the projected changes in CWD stock, the mean respiration rate was  $1.2 \pm 0.3 \mu\text{mol m}_g^2 \text{ s}^{-1}$  (2001–2006). A partial resurvey of the CWD plots (diameter  $> 30 \text{ cm}$ ) in July 2006 found that the stock of large CWD was reduced by 22%, from  $25.8 \pm 4.2$  to  $20.2 \pm 4.6 \text{ Mg C ha}^{-1}$ . This partial resurvey CWD is in very good agreement with the estimated loss of total CWD and supports the modeled total CWD respiration rates for 2001–2006.

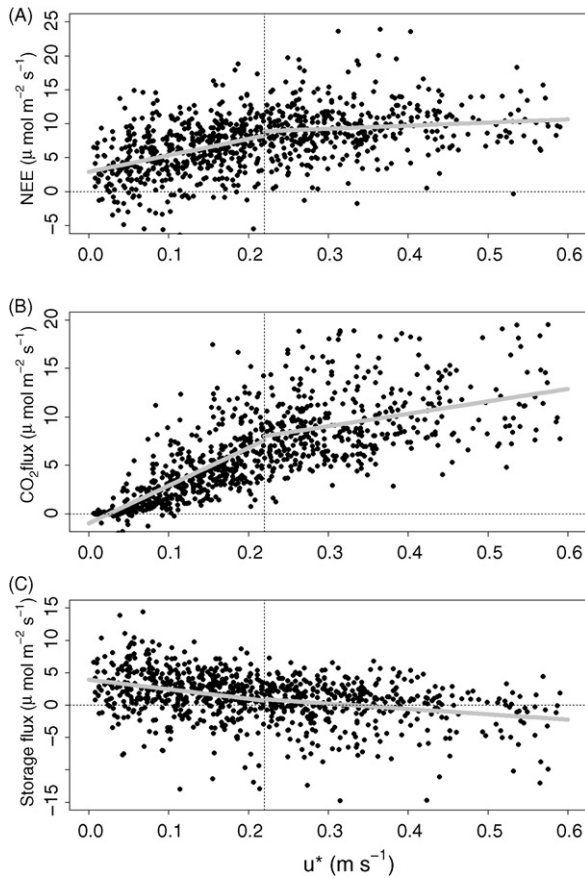
Combining the respiration estimates for the individual components, our best bottom-up estimate for the annual mean  $R_{eco}$  was  $7.6 \mu\text{mol m}_g^2 \text{ s}^{-1}$ . In one of the few other attempts to estimate  $R_{eco}$  using bottom-up methods in the Amazon, Chambers et al. (2004) reported a mean  $R_{eco}$  of  $7.8 \mu\text{mol m}_g^2 \text{ s}^{-1}$  for a primary forest near Manaus, Brazil. However, our local, bottom-up estimate should be considered a lower bound on



**Fig. 1 – (A) Independent estimates of annual ecosystem respiration.** The ‘best estimate’ is based on 4 years of  $u^*$  filtered, gap filled, nighttime flux measurements. The  $^{222}\text{Rn}$  estimate is derived based on similarity to  $\text{CO}_2$  flux (Martens et al., 2004). The light curve intercept value is based on the fit between daytime PAR and NEE (no  $u^*$  filter). The bottom-up estimate includes the major components of the forest respiration budget (the sum is a lower bounds estimate on total respiration). (B) Alternative estimate of ecosystem respiration based on (1) exclusion of storage (flux-only,  $u^*$  filter applied); (2) no  $u^*$  filtering (flux + measured storage); (3) flux-only (no storage and no  $u^*$  filter). (C) Respiration estimates based on measured  $\text{CO}_2$  flux and modeled storage with the  $S_I$  and  $S_d$  storage models (no  $u^*$  filters applied).



**Fig. 2 – (A) Independent estimates of annual net ecosystem exchange (carbon balance) averaged from 2001 to 2005. The ‘best estimate’ is based on  $u^*$  filtered, gap filled flux measurements. The bottom-up biometry estimate is the result of repeated biometric surveys of forest structure (growth, recruitment, mortality). (B) Alternative estimates of the net carbon balance based on (1) exclusion of storage (flux-only,  $u^*$  filter applied); (2) no  $u^*$  filtering (flux + measured storage); (3) flux-only (no storage and no  $u^*$  filter). (C) Carbon balance estimates based on measured  $CO_2$  flux and modeled storage flux through the  $S_b$ ,  $S_d$ , and diurnally varying storage models (DVSM) (no  $u^*$  filter applied).**



**Fig. 3 – Relationship between  $u^*$  and NEE (turbulent  $CO_2$  flux and storage flux) (A) turbulence  $CO_2$  flux (B) and canopy storage (C) for January–April 2004.**

respiration since it does not include any contribution from the large amount of respiring organic material stored aboveground (e.g. rotting tree cores, termite nests, decomposition of suspended leaf litter, etc.). The components of the respiration budget included in this analysis are the largest in magnitude (Chambers et al., 2004) and most amenable to direct measurement and scaling. The bottom up estimate of  $R_{eco}$  cannot be estimated with better temporal resolution than annual mean because some of the terms in the respiration budget have significant seasonal variations and deviations from steady state that are not adequately quantified. A meaningful confidence interval could not be calculated for the bottom-up respiration estimate due to the compilation of wide array of data sets including published data without reported error estimates.

**3.1.2. Net carbon fluxes**

To assess the net carbon balance in the  $TNF_{67}$  from the bottom-up, we repeatedly surveyed almost 3000 trees in 1999, 2001, and 2005. Between 2001 and 2005, the time interval which most closely overlaps with the Eddy-covariance time series, the mean total aboveground biomass was  $192 \pm 5 \text{ Mg C ha}^{-1}$  (trees with diameters  $\geq 10 \text{ cm}$  and  $CWD \geq 2 \text{ cm}$ ), with  $\sim 79\%$  alive and 21% dead. The mean aboveground growth, recruitment (in-growth of new individual trees), and mortality rates were  $3.2 \pm 0.2$ ,  $0.45 \pm 0.05$  and  $3.0 \pm 0.4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ , respectively. Dividing the live aboveground biomass pool by inputs (growth + recruitment) or the outflow (mortality) gave notably short turnover times, 39 and 48 years, respectively, indicating a very dynamic forest (see Pyle et al., submitted for publication for further discussion).

The net flux in live biomass (growth + recruitment – mortality) was  $-0.6 \pm 0.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ , representing a

small net uptake from the atmosphere. The net flux in dead biomass (mortality inputs – respiration) was  $2.2 \pm 0.8 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ , a sizable carbon loss to the atmosphere. The overall mean net carbon flux (net live flux + net dead flux) from this bottom-up budget was therefore  $1.5 \pm 0.6 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  ( $0.41 \pm 0.15 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , carbon loss to the atmosphere), Fig. 2, panel A (additional discussion of Fig. 2 follows in Section 3.5). This result confirms the earlier findings of  $1.9 \pm 1.0 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  carbon loss from this site based on the 1999 and 2001 surveys. Further, this result is consistent with the hypothesis, proposed in Rice et al. (2004), that the TNF site is recovering from a prior disturbance. We have observed a decreasing stock of CWD, high growth rates, increasing biomass, and reversal of the sign of the annual NEE measured by Eddy-covariance over the 4-year interval (Hutyra et al., 2007; Pyle et al., submitted for publication).

### 3.2. Evidence of lost nighttime flux

As a biological process, nighttime  $R_{\text{eco}}$  should not depend on atmospheric turbulence. Under ideal conditions, the measurements of nighttime NEE ( $\text{CO}_2$  flux + storage) would show no relationship with turbulence, but at many forest sites ideal conditions are not met and some flux is not accounted for (Fig. 3). Hence, measurements of canopy  $\text{CO}_2$  storage and flux at the top of the tower are in fact strongly related to the occurrence of turbulence. This is not a surprising result. During periods of weak turbulence, the assumption of horizontal homogeneity required for Eddy-covariance may not be met and horizontal advection can result in 'lost flux' (Massman and Lee, 2002). Our data shows a decrease in  $\text{CO}_2$  flux and an increase in storage flux under low turbulence nighttime conditions, but there was a pronounced reduction in nighttime NEE (the sum of these terms) when turbulence was less than  $0.22 \text{ m s}^{-1}$  (Fig. 3).

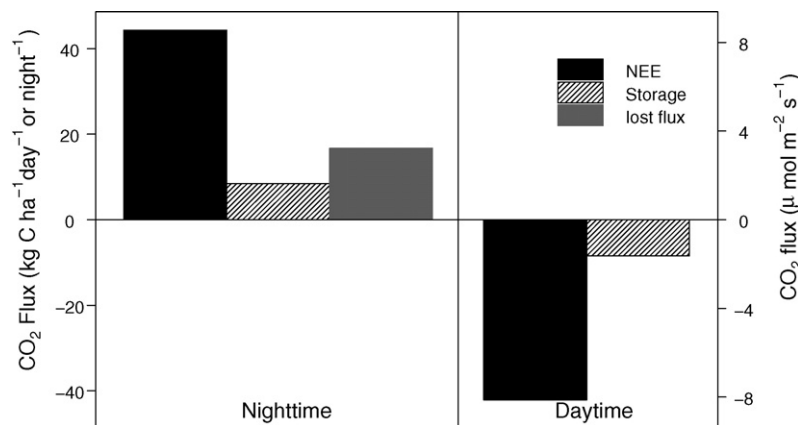
On average, storage flux was negative (venting) and  $\text{CO}_2$  flux was enhanced under windy nighttime conditions ( $u^* > 0.3 \text{ m s}^{-1}$ ). The sum of the two terms appears to have little trend with  $u^*$  (Fig. 3). To correct for the flux lost under low turbulence conditions, a  $u^*$  filter ( $u^* \leq 0.22 \text{ m s}^{-1}$ ) was applied

to remove periods with an apparent low bias, and data gaps were filled to maintain a complete time series (see Hutyra et al. (2007), Hutyra (2007), and Saleska et al. (2003) for further information on gap filling details and on the determination of an objective  $u^*$  threshold). From January 2002 to January 2006, the mean lost nocturnal flux was  $16 \text{ kg C ha}^{-1} \text{ night}^{-1}$ , approximately 40% of the nocturnal respiration flux (Fig. 4). Figs. 1 and 2, panels B, also show the bias if no flux correction is applied.

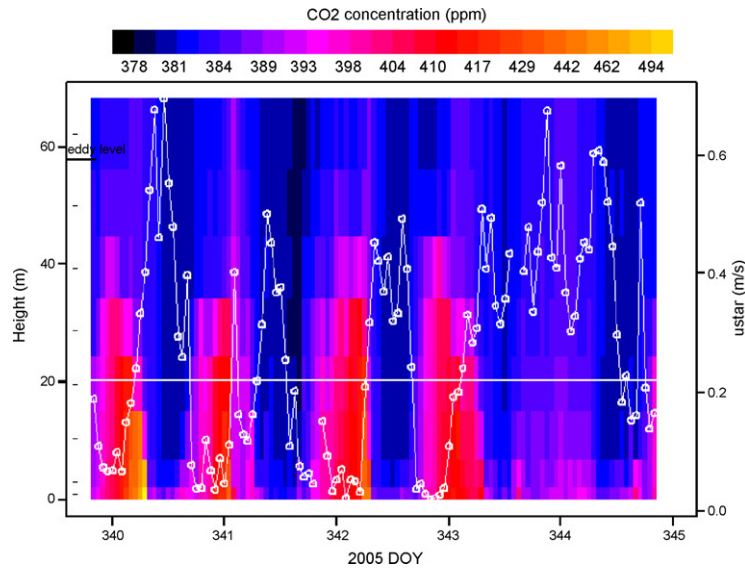
### 3.3. Canopy $\text{CO}_2$ storage

Canopy  $\text{CO}_2$  storage varies diurnally and as a function of boundary-layer turbulence (Figs. 5 and 6). Fig. 5 shows the canopy  $\text{CO}_2$  concentrations and friction velocity ( $u^*$ ) for a typical 5-day period in December 2005. Below the mean canopy height (40–45 m), nocturnal build-up of  $\text{CO}_2$  approaches 100 ppm when  $u^*$  drops to near zero (DOY 340–343, Fig. 5). During the night of December 9, 2005 (DOY 344) high atmospheric turbulence ( $u^* > 0.22 \text{ m s}^{-1}$ ) resulted in a nearly well-mixed canopy profile and no significant build-up of  $\text{CO}_2$ . During the daytime, well-mixed conditions are prevalent with a significant draw-down in canopy  $\text{CO}_2$  concentration resulting from a combination of mixing with low- $\text{CO}_2$  air from aloft and carbon uptake through photosynthesis (Fig. 5). Turbulence and canopy storage were strongly negatively correlated, with storage lagging turbulence by approximately 1 h ( $R^2 = 0.75$ , Fig. 6). However, as shown in Fig. 5 conditions can vary substantially from day to day and night to night.

Gaps in canopy storage measurements are common at many forest flux tower sites, particularly in areas with extreme climate such as in tropical (very high temperatures and humidity) and boreal forests (very low temperatures and icing). If gaps in storage measurements are not accounted for, significant errors in carbon balance estimates can result (Figs. 1 and 2, B panels). Table 1 shows the mean diel  $S_d$  storage model values and Tables 2 and 3 show the model coefficients for fitting the  $S_t$  model for canopy storage at TNF<sub>67</sub>. Fig. 7 illustrates the relationship between measured accumulated



**Fig. 4** – Mean accumulated nighttime (1800–0500, LT) and daytime (0600–1700, LT)  $u^*$  corrected NEE, storage and 'lost' nocturnal flux for 2002–2006. The mean 24-h storage flux is zero, with  $8.4 \text{ kg C ha}^{-2} \text{ night}^{-1}$  accumulating during the nighttime and  $-8.4 \text{ kg C ha}^{-2} \text{ daytime}^{-1}$  venting during the daytime. The mean 'lost' nocturnal flux (the difference between  $u^*$  corrected and uncorrected nighttime fluxes) was  $16.7 \text{ kg C ha}^{-2} \text{ nighttime}^{-1}$ .

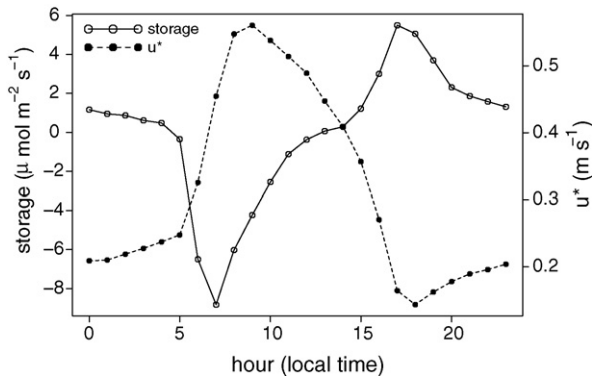


**Fig. 5 – Hourly canopy CO<sub>2</sub> profile concentration (ppm) measurements interpolated across eight measurement heights (62.2, 50.1, 39.4, 28.7, 19.6, 10.4, and 0.9 m) for days of year 340–345 (local time) in 2005. Canopy friction velocity ( $u^*$ ) is shown in the open circle points. The horizontal line at  $0.22 \text{ m s}^{-1}$  denotes the  $u^*$  threshold for data filtering to correct for lost flux. Note that the same time periods are illustrated in Figs. 5 and 8, with the high-turbulence night on DOY 344 illustrating the influence of turbulence on canopy CO<sub>2</sub> storage.**

nighttime storage and the time-weighted  $u^*_{*w}$  parameter used in formulating the  $S_I$  model ( $n = 1319$  nights,  $R^2 = 0.37$ ). A seasonal difference in the linear relationship between the weighted turbulence ( $u^*_{*w}$ ) and storage might be expected, but the seasonal model fits were statistically indistinguishable (Table 1) and an annual model was utilized for subsequent analysis. The overall model fit at the TNF<sub>67</sub> was comparable to the results reported by Iwata et al. (2005) for the Jarú and Caxiunã Amazonian flux tower sites notwithstanding that much less data were available for model calibration at the other flux tower sites. The errors on the diel  $S_d$  model values converged after including approximately 2400 h (100 days) of measured storage data.

Fig. 8 shows a comparison between the  $S_d$  and  $S_I$  models and observations for the same time period represented in Fig. 5. During the nighttime, the  $S_I$  model roughly captured the

accumulated nighttime storage, both under and over-predicting the mean accumulation. The  $S_I$  model represented the morning draw-down and afternoon build-up well, but the results are largely comparable to the much simpler diel  $S_d$  model. The  $S_d$  model did not capture hourly variability (Fig. 8A), but represented the overall mean behavior. Fig. 8B



**Fig. 6 – Observed mean diurnal cycles of canopy friction velocity ( $u^*$ ) and canopy CO<sub>2</sub> storage between 2002 and 2006.**

**Table 1 – Diel storage model,  $S_d$  (Eq. (6)), hourly values**

Local time	Coefficient ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )
0600	$-6.49 \pm 0.22$
0700	$-8.82 \pm 0.25$
0800	$-6.02 \pm 0.20$
0900	$-4.23 \pm 0.15$
1000	$-2.54 \pm 0.13$
1100	$-1.13 \pm 0.10$
1200	$-0.38 \pm 0.08$
1300	$0.07 \pm 0.08$
1400	$0.29 \pm 0.09$
1500	$1.21 \pm 0.09$
1600	$3.00 \pm 0.12$
1700	$5.49 \pm 0.13$
1800	$5.07 \pm 0.14$
1900	$3.7 \pm 0.15$
2000	$2.31 \pm 0.16$
2100	$1.86 \pm 0.16$
2200	$1.57 \pm 0.16$
2300	$1.31 \pm 0.18$
2400	$1.16 \pm 0.19$
0100	$0.95 \pm 0.18$
0200	$0.88 \pm 0.19$
0300	$0.62 \pm 0.19$
0400	$0.48 \pm 0.19$
0500	$-0.35 \pm 0.19$

**Table 2 – Annual and seasonal model coefficient values for total nighttime CO<sub>2</sub> canopy storage in the Iwata et al. (2005) model (Eq. (7))**

	$a_1$	$a_2$	$R^2$	$p$ -Value
Annual model	34.8 ± 0.64	−75.4 ± 2.69	0.37	<0.0001
Dry season model	35.2 ± 0.96	−78.0 ± 4.3	0.39	<0.0001
Wet season model	33.9 ± 0.85	−71.9 ± 3.55	0.34	<0.0001

The dry season extends from day of year 196–349.

shows the daily measured mean nighttime storage averaged for better comparison with the  $S_1$  model. Fig. 8C shows a comparison between the estimated NEE (CO<sub>2</sub> flux + storage) based on the storage models and the measured NEE. The agreement between the modeled and observed NEE data is extremely good, but it is not surprising considering that CO<sub>2</sub> flux is the major term in NEE and differences between measured and modeled storage are small relative to the overall NEE (also see Fig. 4). Overall, both the  $S_1$  and  $S_d$  models did capture the mean storage behavior reasonably well and explained 44% and 54% of the total observed hourly variance in canopy CO<sub>2</sub> storage, respectively. Either of these storage models could be used for deriving fluxes on daily to longer time scale, but should not be taken to represent the hourly storage values accurately or as a total replacement for measuring storage flux.

The  $S_1$  and  $S_d$  models, with parameterizations from the TNF<sub>67</sub> tower site, were tested against the observed storage at the nearby km 83 forest tower site (Miller et al., 2004) and were found to explain significantly less of the observed hourly variance at the nearby site, only capturing 35% and 37%, respectively. The TNF<sub>67</sub> and TNF<sub>83</sub> towers sites are ~16 km apart, with similar flux measurement equipment, and comparable forest structure (Miller et al., 2004; Hutrya et al., 2007). The TNF<sub>83</sub> site has more varied topography and even small differences in microclimate, topography, and/or canopy architecture apparently translate into significant differences in air drainage and wind profile distributions. Given that the parameters for the  $S_1$  and  $S_d$  models were not found to be applicable across these proximate sites, we infer that site-specific model storage parameterizations must be utilized.

**Table 3 – Values of daytime hourly model coefficients ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) for daytime depletion cycle of forest canopy storage based on the annual model (described in Table 2, Eqs. (7) and (10))**

Local time	Coefficient
6:00	−0.34
7:00	−0.45
8:00	−0.31
9:00	−0.21
10:00	−0.12
12:00	−0.05
13:00	−0.02
14:00	0.002
15:00	0.017
16:00	0.06
17:00	0.15
18:00	0.29

### 3.4. Tower-based respiration flux measurements

#### 3.4.1. Best estimates of ecosystem respiration

The validity of Eddy-correlation measurements and adjustments to account for missing flux during calm conditions can be assessed by considering independent estimates of  $R_{\text{eco}}$  and NEE. We considered several alternatives for estimating  $R_{\text{eco}}$  from the Eddy-covariance data (Fig. 1, panel A). During the nighttime hours, NEE represents  $R_{\text{eco}}$ , because photosynthesis is zero. Our best tower-based estimate of  $R_{\text{eco}}$  was  $8.6 \pm 0.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , based on the use of a  $u^*$  filter for the nighttime NEE calculated using hourly measured CO<sub>2</sub> flux and storage from January 2002 to January 2006. Our first alternative estimate derives  $R_{\text{eco}}$  based on the intercept value of a hyperbolic light curve fit (Eq. (6)) to the relationship between daytime NEE and photosynthetically active radiation (PAR) (Fig. 9; see Hutrya et al., 2007). This approach works particularly well at the TNF<sub>67</sub> because no significant temperature relationship was observed for nighttime NEE (Hutrya et al., 2007). The mean light curve intercept value was  $8.9 \pm 0.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , based on all available daytime data ( $\text{PAR} \geq 40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ; no  $u^*$  filter applied), and was statistically indistinguishable from our best estimate of  $R_{\text{eco}}$ ,  $8.6 \pm 0.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . The light curve intercept and nighttime flux measurements are independent since entirely disjoint data were used in the comparison, and no  $u^*$  filter is applied to the daytime data.

Martens et al. (2004) independently assessed raw and  $u^*$  corrected NEE measurements at night at the TNF<sub>67</sub> by comparing CO<sub>2</sub> Eddy-covariance data with CO<sub>2</sub> fluxes inferred from <sup>222</sup>Rn and CO<sub>2</sub> profiles and <sup>222</sup>Rn soil flux measurements. Nighttime NEE derived from <sup>222</sup>Rn was found to average  $9.0 \pm 1.0 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in the wet season and  $6.4 \pm 0.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in the dry season, agreeing very well with  $u^*$  filtered NEE measurements during the same time period ( $8.7 \pm 1.1$  and  $6.6 \pm 0.7$ , respectively) (Martens et al., 2004). Scaling for the length of the local wet and dry seasons, the mean annual respiration rate inferred from the <sup>222</sup>Rn measurements was  $7.9 \pm 0.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$  (Fig. 1, panel A), equivalent to our best estimate within confidence bounds.

#### 3.4.2. Treatments of canopy CO<sub>2</sub> storage

We tested the sensitivity of  $R_{\text{eco}}$  estimates to the treatment of canopy storage and  $u^*$  filtering to quantify possible errors and biases. An estimate of annual mean  $R_{\text{eco}}$  based only on CO<sub>2</sub> flux ( $u^*$  filtered) at the top of the tower (excluding canopy storage measurements) agreed very well with our best estimate of mean  $R_{\text{eco}}$  and the independent estimates (Fig. 1, panel B). Application of the  $u^*$  filter effectively removed nighttime periods of significant canopy CO<sub>2</sub> accumulation due to calm conditions

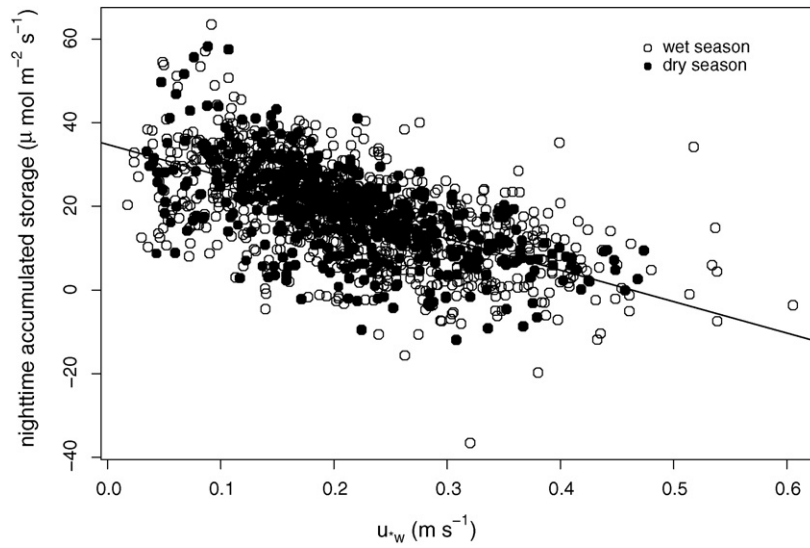


Fig. 7 – Measured nightly  $u_w$  (time-weighted friction velocity) plotted against total nighttime accumulated canopy storage (2002–2006) with the filled circles denoting the dry season and the open circles denoting the wet season. No significant seasonal difference was detected. The solid line is the linear best fit ( $R^2 = 0.37$ ).

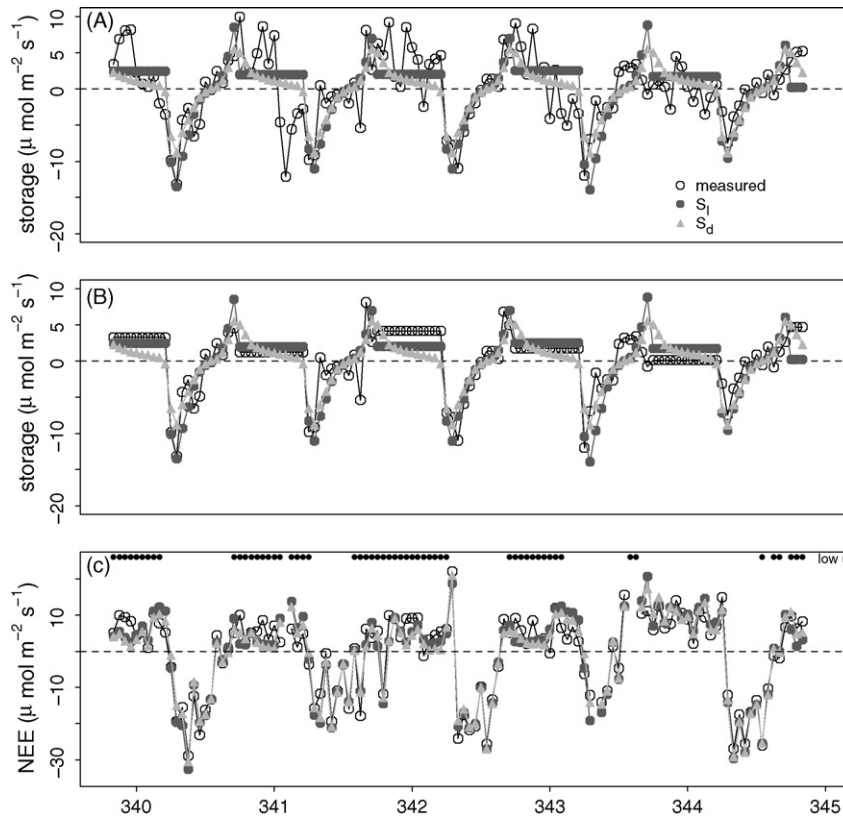
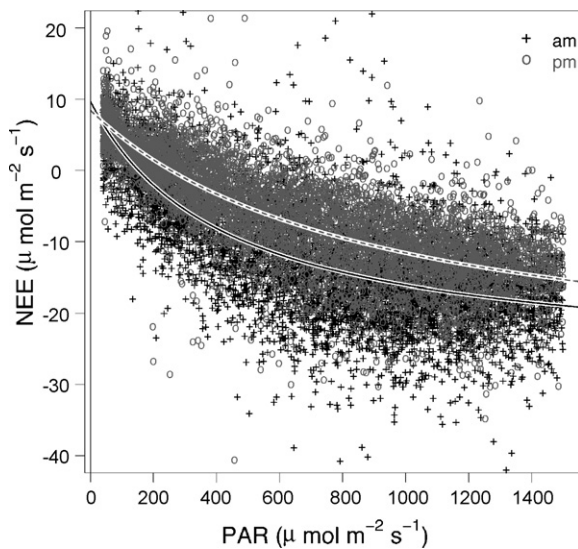


Fig. 8 – Time series comparison for measured and modeled canopy  $CO_2$  storage and NEE for days of year 340–345 (local time) in 2005. The  $S_d$  and  $S_t$  storage models showed good agreement with the hourly measured storage (A) and with the nighttime mean storage (B). Measured NEE ( $CO_2$  flux + storage) and estimated NEE ( $CO_2$  flux + modeled storage) also agreed well (C). The points along the top of panel C indicate hours with low turbulence ( $u^* < 0.22 m s^{-1}$ ) which would be removed through filtering in the ‘best estimates’ of NEE and R. Note that the same time periods are illustrated in Figs. 5 and 8, with the night on DOY 344 highlighting the influence of turbulence on canopy  $CO_2$  storage.



**Fig. 9** – Net ecosystem exchange of CO<sub>2</sub> (NEE,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) as a function of photosynthetically active radiation (PAR,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), January 2002–January 2006. Two separate nonlinear least squares approximation (hyperbolic function) are plotted through the data for the morning (PAR > 40 and before 1200) and afternoon periods (PAR > 40 and after 1200). The vertical line denotes  $0 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR. The morning (cooler, moister and dashed line) and afternoon (warmer, drier and solid line) intercept values were statistically indistinguishable at  $9.68 \pm 0.98$  and  $8.43 \pm 0.56 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The overall intercept value (all data PAR >  $40 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) was  $8.9 \pm 0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ .

(see Fig. 5). However, the combination of excluding storage and applying a  $u^*$  filter, introduced a serious temporal bias when integrating diurnally, since CO<sub>2</sub> accumulated and vented at different times of the day (Figs. 4–6). The overall mean nighttime measured storage was  $1.2 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ . When a  $u^*$  filter was applied, the periods of accumulation are removed and the mean nighttime storage was reduced to only  $-0.18 \pm 0.11 \mu\text{mol m}^{-2} \text{s}^{-1}$ . But, during the daytime filtering is not effective in removing the (negative) accumulation from the previous night, due to the predominance of well-mixed conditions; the mean daytime canopy storage was  $-2.1 \pm 0.04 \mu\text{mol m}^{-2} \text{s}^{-1}$  and applying a  $u^*$  filter only changed the estimated storage value slightly to  $-2.4 \pm 0.08 \mu\text{mol m}^{-2} \text{s}^{-1}$ .

Hence, using only  $u^*$  filtered flux (no storage), we obtained a reasonable  $R_{\text{eco}}$  value, but the 24-h mean NEE was strongly biased because of correlation between  $u^*$  and storage (i.e., daytime NEE was biased positive, Figs. 1, 2 and 6). This result is consistent with the finding by Papale et al. (2006) in European temperate forests. The accumulation of CO<sub>2</sub> in the canopy, which was excluded by using only the flux (no storage) and a  $u^*$  filter, is released during the daytime hours and must therefore be carefully included in carbon budget computations. Omitting storage also strongly affected the light curve, biasing estimates of  $R_{\text{eco}}$  due to the morning and evening patterns in storage (Figs. 6 and 9); without the inclusion of storage, the intercept value was reduced to only  $6.9 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (daytime data, no  $u^*$  filter), significantly underestimating the  $R_{\text{eco}}$ .

Both the  $S_1$  and  $S_d$  models for canopy storage result in an underestimation of  $R_{\text{eco}}$ , due to the models' inability to adequately account for the influence of turbulence on nighttime storage (Fig. 1, panel C). The overall mean nighttime storage for  $S_1$  and  $S_d$  models was 1.5 and  $1.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively, comparable to the observed mean storage without a  $u^*$  filter, but the design of these models does not allow for lost flux corrections, such as  $u^*$  filtering. The mean observed respiration (CO<sub>2</sub> flux + measured storage) without the inclusion of a  $u^*$  filter, but using fluxes plus  $S_1$  or  $S_d$ , was only  $\sim 6.4 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Fig. 1, panel C). Not surprisingly, the estimates based on the modeled storage and measured CO<sub>2</sub> flux were consistent with the unfiltered nighttime NEE measurements (Fig. 1, panel B). However, nighttime NEE based on the  $S_1$  and  $S_d$  models did not agree with independent estimates of respiration from  $u^*$  filtered NEE, <sup>222</sup>Rn, bottom-up, or light-curve intercept (Fig. 1, panel A).

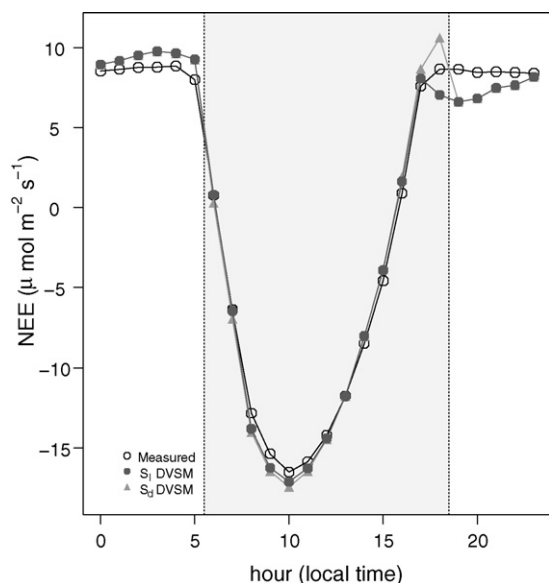
### 3.5. Tower-based net ecosystem exchange measurements

Mean daily NEE (24-h average summing photosynthesis and respiration) observed at this site was  $0.25 \pm 0.04 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $u^*$  filtered, including measured storage, January 2002–January 2006) and agreed within errors with the independent bottom-up estimate of  $0.41 \pm 0.15 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Fig. 2, panel A). Mean NEE without the inclusion of a  $u^*$  filter was  $-0.9 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ , as in the case of respiration, this value did not agree with independent estimates due to biases from missing nighttime respiration (Fig. 2, panel B and Fig. 4). NEE based on measured flux and modeled storage (no  $u^*$  filter) also resulted in a large estimated carbon sink, again due to biases from missing nighttime flux (Fig. 2, panel C). The mean CO<sub>2</sub> flux (no storage included) measured at the top of the tower was  $0.8 \pm 0.1$  or  $-0.9 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  with and without the inclusion of a  $u^*$  filter, respectively. Entirely excluding storage during both the daytime and nighttime resulted in a severe bias due to the combined effects of missing nighttime storage and daytime venting of nocturnal accumulations within the canopy.

When integrated across 24 h, application of a  $u^*$  filter does not negate the need for storage measurements since it excludes periods of significant CO<sub>2</sub> accumulation within the canopy (nighttime), but includes the subsequent daytime venting (negative storage), resulting in a strong bias. Failing to apply a  $u^*$  filter to fluxes, without storage, also gave biased results.

### 3.6. Diurnally varying storage models

We devised and tested a diurnally varying storage model (DVSM) for estimating NEE when storage was missing. In the DVSM formulation, days and nights were treated separately to allow for different storage patterns. During the nighttime (local time 1800–0600), we estimated NEE using only CO<sub>2</sub> flux measurements (no storage) from well mixed times which allowed for accurate estimation of nighttime respiration (see Section 3.4.2). But, during the daytime (local time 0600–1800), canopy storage model coefficients were included in the NEE estimate (CO<sub>2</sub> flux + storage) to capture the venting of nighttime storage accumulation. Both the  $S_1$  and  $S_d$  DVSM were able to accurately estimate the daytime venting of stored CO<sub>2</sub>, and



**Fig. 10 – Diurnal cycle of NEE comparing measured (‘best estimate’) with the  $S_1$  and  $S_d$  diurnally varying storage models (DVSM). In the DVSM days and nights were treated separately to allow for different storage patterns. During the nighttime (local time 1800–0600) NEE was estimated using only  $\text{CO}_2$  flux measurements (no storage) from well mixed times ( $u^* \geq 0.22 \text{ m s}^{-1}$ ) and during the daytime (local time 0600–1800) canopy storage models were included in the NEE estimation ( $\text{CO}_2$  flux + storage) to capture the venting of accumulated  $\text{CO}_2$  from the previous night.**

the mean net carbon balance agreed well with the independent estimates (Figs. 1, 2 and 10). Both  $S_1$  and  $S_d$  DVSMs produced comparable results, with the error on both models maximizing at sunset due to the highly variable and quickly changing conditions during that time.

#### 4. Conclusions and implications

In this paper we derived four independent estimates for NEE and  $R_{\text{eco}}$  (Eddy flux with  $u^*$  filter; Eddy flux daytime data extrapolated to zero light; similarity with  $^{222}\text{Rn}$ ; and bottom-up), providing rigorous tests for Eddy-covariance estimates of  $R_{\text{eco}}$  using conventional  $u^*$  filtered, nighttime flux data. The four methods were in close agreement for both the ecosystem carbon budget (Fig. 1) and for  $R_{\text{eco}}$  (Fig. 2) within confidence intervals. We then examined the biases potentially associated with computations that do not account for lost nighttime flux or that have missing storage measurements. The results show that these biases must be addressed at any site employing the Eddy-covariance technique, with special attention in tropical forests.

$R_{\text{eco}}$  estimated using only  $\text{CO}_2$  flux (applying a  $u^*$  filter, excluding canopy storage) at the top of the tower also agreed with our best estimate and with the independent validations (Fig. 1, panel B). However, flux-only estimates of NEE were biased when examined on a 24-h basis (Fig. 2, panel B), with or

without a  $u^*$  filter. If no  $u^*$  filter was applied to flux-only data, nighttime  $R_{\text{eco}}$  was far too low and NEE was negatively biased. Applying a  $u^*$  filter to flux-only data at night,  $R_{\text{eco}}$  was well represented, but NEE during the day was positively biased. Utilizing the  $S_1$  and  $S_d$  canopy storage models throughout the day and night resulted in an underestimate of  $R_{\text{eco}}$  due to unaccounted for nighttime ‘lost flux’. Both canopy storage models tested here were based only on the bulk mean hourly or nightly storage accumulation patterns and could not account for short-term and diurnal changes associated with turbulence. On a daily or longer basis the storage models agree reasonably well with observations, but did not allow for filtering based on turbulence or other corrections for the known lost nocturnal flux. We conclude that the basic procedure for utilizing a  $u^*$  filter produces a reliable carbon budget at our site, and we would expect this procedure should work comparably well at similar sites with low relief, a moderate percentage of turbulent hours, and good measurements of storage.

We derived and tested a diurnally varying canopy storage model to estimate NEE at sites that lack direct canopy storage measurements. Our method corrects for lost nocturnal flux by using measurements from turbulent time periods and captures the daytime venting of nocturnally accumulated  $\text{CO}_2$  through the incorporation of the average daytime storage profile. At our site we found that storage model errors converged with approximately 100 days of data. However, model parameters were site-specific. At a minimum, short-term measurements of storage must be available to develop a DVSM and allow for extensive data recovery at sites where canopy  $\text{CO}_2$  storage is not routinely measured.

The robust correction approaches that we have critically examined here provide a method to utilize and integrate flux measurements from the multitude of flux tower sites where storage is not routinely measured. We have shown that it is possible to correct and validate nighttime data for the ubiquitous ‘lost’ nighttime flux, providing knowledge of ecosystem carbon exchange across a wide range of ecosystems. It is clear, however, that large biases can impact Eddy flux data if the measurements are not subjected to meticulous analysis, careful corrections, and rigorous error analysis. The analytical framework laid out in this paper can serve as a general template for validation and assessment of biases in flux measurements at other flux tower sites across the globe.

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