BIOMETRIC AND MICROMETEOROLOGICAL MEASUREMENTS OF TROPICAL FOREST CARBON BALANCE

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Abstract. We used two independent approaches, biometry and micrometeorology, to determine the net ecosystem production (NEP) of an old growth forest in Pará, Brazil. Biometric inventories indicated that the forest was either a source or, at most, a modest sink of carbon from 1984 to 2000 ($+0.8 \pm 2$ Mg C·ha^{-1}·yr^{-1}; a positive flux indicates carbon loss by the forest, a negative flux indicates carbon gain). Eddy covariance measurements of CO_2 exchange were made from July 2000 to July 2001 using both open- and closed-path gas analyzers. The annual eddy covariance flux calculated without correcting for the underestimation of flux on calm nights indicated that the forest was a large carbon sink (-3.9 Mg C·ha^{-1}·yr^{-1}). This annual uptake is comparable to past reports from other Amazonian forests, which also were calculated without correcting for calm nights. The magnitude of the annual integral was relatively insensitive to the selection of open- versus closed-path gas analyzer, averaging time, detrending, and high-frequency correction. In contrast, the magnitude of the annual integral was highly sensitive to the treatment of calm nights, changing by over 4 Mg C·ha^{-1}·yr^{-1} when a filter was used to replace the net ecosystem exchange (NEE) during nocturnal periods with $u^* < 0.2$ m/s. Analyses of the relationship between nocturnal NEE and u^* confirmed that the annual sum needs to be corrected for the effect of calm nights, which resulted in our best estimate of the annual flux ($+0.4$ Mg C·ha^{-1}·yr^{-1}). The observed sensitivity of the annual sum to the u^* filter is far greater than has been previously reported for temperate and boreal forests. The annual carbon balance determined by eddy covariance is therefore less certain for tropical than temperate forests. Nonetheless, the biometric and micrometeorological measurements in tandem provide strong evidence that the forest was not a strong, persistent carbon sink during the study interval.

Key words: biosphere–atmosphere exchange; CO_2 exchange; eddy covariance; LBA; net ecosystem production; tropical forest.

INTRODUCTION

Several recent reports indicate that undisturbed forest stands in Amazonia are sequestering large amounts of carbon. These observations are surprising, since primary forest is generally considered to be in equilibrium with the atmosphere (Waring and Schlesinger 1985), and important, since they may significantly change understanding of the global carbon budget (Malhi et al. 1999). Forest carbon balance can be measured using either of two independent approaches: biometry or micrometeorology. Based on integrated micrometeorology, Grace et al. (1995) reported a moderate carbon sink for a stand in Rondônia (-1.0 Mg C·ha^{-1}·yr^{-1}), and Malhi et al. (1998) reported a large sink for a stand outside of Manaus (-5.9 Mg C·ha^{-1}·yr^{-1}). Andreae et al. (2002) reiterated these results using longer datasets at these sites, and three additional flux towers in Amazonia, that all indicated uptake of -3 to -7 Mg C·ha^{-1}·yr^{-1}. In contrast, based on biometry, Phillips et al. (1998) reported a smaller sink of -0.6 ± 0.4 Mg C·ha^{-1}·yr^{-1} for 97 tropical stands. The discrepancy between moderate uptake observed with biometry and large uptake observed using towers, as well as the uncertainty of integrated tower measurements for tropical forest, remain unresolved issues (Malhi et al. 1998, Kruijt et al. 2004).

Eddy covariance is a micrometeorological technique that provides half-hour observations of the net CO_2 exchange between a forest stand and the atmosphere (Baldocchi et al. 1988). Wofsy et al. (1993) pioneered the use of integrated eddy covariance to determine ecosystem carbon balance, an approach that has been subsequently applied to many temperate forests (e.g., Valentini et al. 2000). Annually integrated eddy covariance is often reported to have an uncertainty of 0.5 Mg C·ha^{-1}·yr^{-1} (Watson 2000), though this accuracy is almost certainly site specific, and analyses supporting this claim have been published for only a few sites (Goulden et al. 1996, Moncrieff et al. 1996, Aubinet et al. 2000). Barford et al. (2001) reported good agree-

PLATE 1. Eddy covariance tower (height = 64 m) at km83, Tapajós National Forest, Pará, Brazil. Photo Credit: Marcy Litvak.

ment between tower-based and biometry-based measurements of carbon balance for a temperate forest, providing evidence that annually integrated eddy covariance is accurate at some sites. Nonetheless, because the integrated eddy flux is the small difference between two large numbers (daytime CO_2 uptake and nighttime CO_2 efflux), there is reason to suspect that the agreement reported by Barford et al. (2001) may not hold at all sites. In particular, the tall vegetation, calm winds, and year-round growing season that are characteristic of tropical forest may exaggerate the effects of the day-to-night measurement bias, and increase the uncertainty of annual flux integrals.

We used eddy covariance to measure the CO_2 exchange between the atmosphere and a primary tropical forest in Pará, Brazil from July 2000 to July 2001 as part of the Large-scale Biosphere–Atmosphere Experiment in Amazonia (LBA). We integrated these observations using several approaches to provide a tower-based analysis of forest carbon balance. Additionally, we compared tree inventories at the same location performed in 1984 and 2000 to provide a biometry-based measurement of forest carbon balance. In this paper, we compare the results from these two approaches and analyze the uncertainties in the tower-based observations. A companion paper by Goulden et al. (2004) discusses the physiological controls on diel and seasonal CO_2 exchange at the site. A second companion paper by da Rocha et al. (2004) discusses the diel and seasonal patterns of water and energy exchange at the site.

METHODS

Site

The measurements were made at the FLONA Tapajós km 83 tower site (see Plate 1), ~70 km south of Santarém, Pará (3.01030° S, 54.58150° W). The vegetation was closed tropical forest with canopy emergents (canopy height ~35–40 m) on flat upland terrain (Hernan-

dez Filho et al. 1993). The site was selectively logged in September 2001, but all of the observations reported here were made prior to logging, while the forest was still considered old growth. Forest extended 5 km to the east, 8 km to the south, and 40 km to the north before reaching pasture. The site was on a flat plateau (the planalto) that extended many kilometers to the north, south, and east. Forest continued 8 km west to the edge of the planalto before dropping to the Tapajós River 14 km from the tower. The total relief within 1–2 km of the tower was ~10 m, with occasional 10–30 m deep stream gullies farther from the tower.

Ground-based inventories

Biomass inventories can be used to directly measure carbon stocks and assess the net carbon balance during a several-year interval. We used three inventories spanning 16 yr to determine the carbon balance of the forest in the area of the tower.

The first survey was made in 1984 by the Brazilian forest service, Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis Brasília (IBAMA), which inventoried 3200 ha in the Tapajós National Forest (Fig. 1, referred to as the IBAMA survey). The survey area was divided into 48- or 50-ha blocks, and trees with diameter at breast height (dbh) > 55 cm were identified to common name, measured, tagged, and mapped. The second survey was made in 2000 in preparation for selective logging and included 700 ha (the TREVISO survey). Both the 1984 IBAMA and 2000 TREVISO surveys included the 48-ha block where the eddy flux tower was located (block 10b in Fig. 1). The third survey was made in March 2000 by the authors of this paper (the UCI survey). The UCI survey focused on an 18-ha (300 m north–south × 600 m east–west) area within block 10b and directly east (upwind) of the tower (Fig. 1). The UCI survey identified, measured, tagged, and mapped all trees with dbh > 35 cm (Fig. 1). Additionally, trees with 10 cm < dbh < 35 cm were surveyed in three 600 × 10 m (1.8 ha total) east–west transects within the 18-ha intensive survey plot.

The spatial overlap between the TREVISO and UCI surveys was established by comparing the two sets of tags on overlapping trees. The spatial overlap between the IBAMA and later surveys was determined to within 50–100 m by comparing the locations of 175 trees with tags that remained legible from the original 1984 IBAMA survey. We used the IBAMA and TREVISO data from block 10 (block 10b; Fig. 1) and the allometric equations reported by Keller et al. (2001) to calculate the aboveground biomass of trees with dbh > 55 cm in 1984 and 2000.

All three of the surveys neglect some of the smaller classes of plants, which may contain significant carbon. For the 1984 IBAMA and 2000 TREVISO surveys, the biomass in trees with 15 cm < dbh < 55 cm was
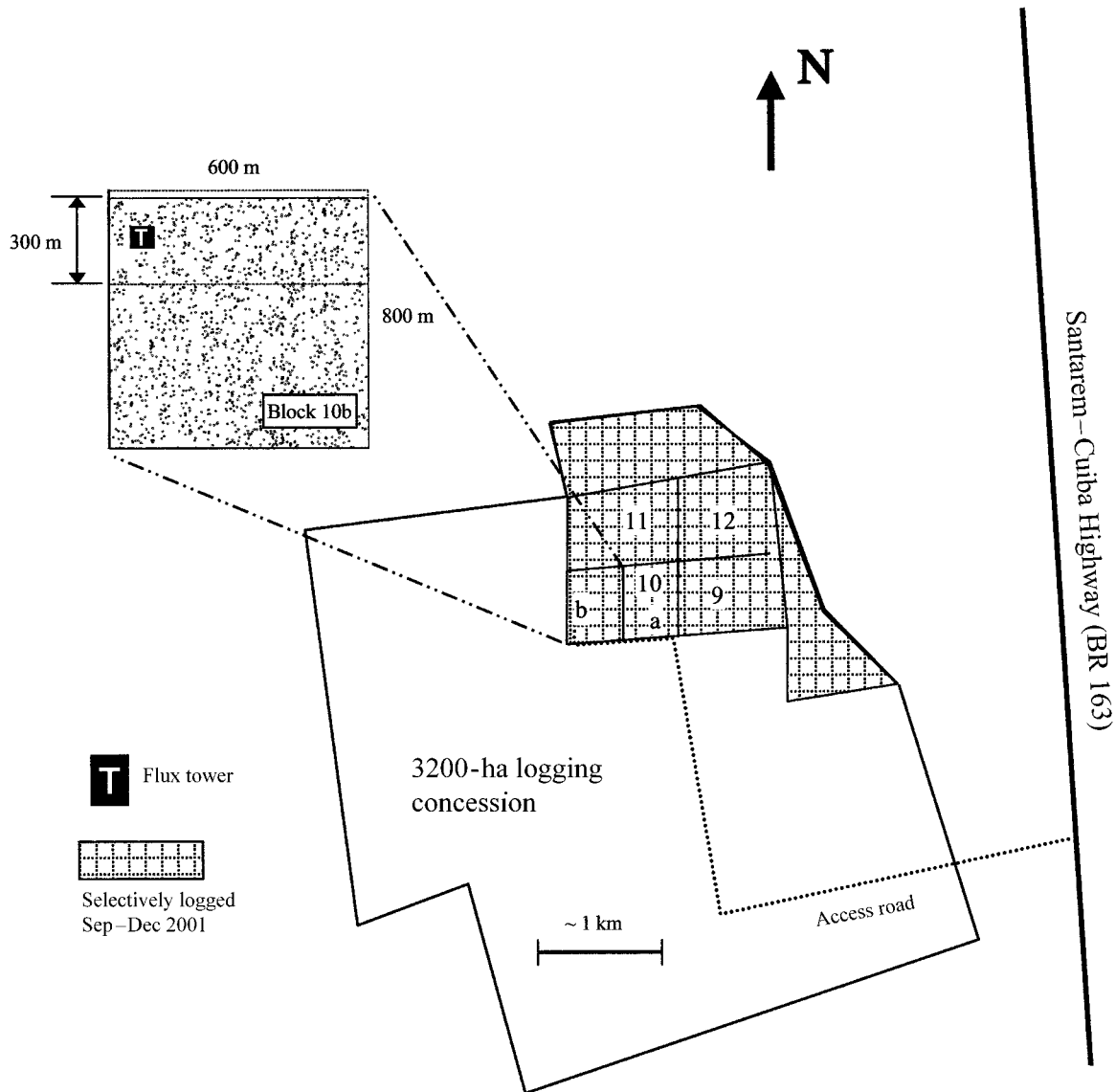
FIG. 1. Site layout: Tapajós National Forest, Pará, Brazil. The shaded area denotes the ~700-ha portion of the 3200-ha logging concession logged September through December 2001. All measurements reported here were taken before the logging began. The location of the eddy flux tower is denoted by the ''T'' in block 10b. Filled circles denote locations of trees with dbh > 55 cm from the 48-ha 2000 TREVISO block 10b survey.

estimated based on the UCI survey's ratios of biomass in the various size classes (Table 1). The biomass of vines, epiphytes, and trees with dbh < 15 cm was estimated using the result of Keller et al. (2001) that their combined biomass was 26% of the biomass of all trees with dbh > 15 cm. These data were then summed to calculate the total aboveground live biomass (AGLB), and to determine the net biomass increment between surveys.

We estimated the uncertainty in the net biomass increment using a sensitivity analysis of hypothesized errors. We determined the sensitivity of net biomass increment to a hypothesized change in tree demography and an increase in small diameter plants (Phillips et al. 2002) by recalculating AGLB for the 1984 IBAMA survey assuming the biomass in all plants with dbh < 55 cm had increased or decreased by 20% between surveys. The associated uncertainty was ±1.2 Mg C·ha^{-1}·yr^{-1}. Additionally, we determined the sensitivity of net biomass increment to a hypothesized difference between surveys in the treatment of buttressed trees by recalculating AGLB for the 1984 IBAMA survey assuming the DBH of all buttressed trees was overestimated by 30%. The associated uncertainty was ±0.2

TABLE 1. Biomass inventories at Tapajós National Forest at kilometer 83.

Inventory	Pool	Area (ha)	No. trees	Trees/ha	Carbon† (Mg C/ha)
1984 IBAMA	dbh > 55 cm	48	1056	22	84
	35 cm < dbh < 55 cm‡	...	...	...	28
	15 cm < dbh < 35 cm‡	...	...	...	44
	dhb < 15 cm, vines, and epiphytes§	...	...	...	41
	total estimated AGLB (1984)‖	...	...	...	197
2000 TREVISO	dbh > 55 cm	48	1006	21	79
	35 cm < dbh < 55 cm‡	...	...	...	27
	15 cm < dbh < 35 cm‡	...	...	...	41
	dhb < 15 cm, vines, and epiphytes§	...	...	...	38
	total estimated AGLB (2000)	...	...	...	185
2000 UCI	dbh > 55 cm	18	423	24	89
	35 cm < dbh < 55 cm	18	568	32	30
	15 cm < dbh < 35 cm	1.8	445	247	47
	dhb < 15 cm, vines, and epiphytes§	...	...	...	38
	total estimated AGLB (2000)	...	...	...	204

† We assumed that carbon accounted for 49% of the biomass (Chambers et al 2001).

‡ Using the AGLB component ratios as measured in the 2000 UCI survey.

§ Following Keller et al. (2001), who found the biomass in small trees with dbh < 15 cm, vines, and epiphytes totaled 26% of the biomass of all trees with dbh > 15 cm.

‖ Aboveground live biomass.

Mg C·ha^{-1}·yr^{-1}. The overall uncertainty of net biomass increment was therefore calculated as ±1.5 Mg C·ha^{-1}·yr^{-1}.

Tower measurements

The net ecosystem exchange (NEE) was calculated for each half-hour interval as the sum of the turbulent CO_2 flux at 64 m (the eddy flux) and the change in the amount of CO_2 in the air column beneath 64 m (the storage flux). The measurements were made from a 67 m tall, 46 cm triangular cross section tower (model 55G; Rohn, Peoria, Illinois, USA). For the turbulent flux, the wind vector and speed of sound were measured at 64 m with a three-axis sonic anemometer pointed east (Campbell Scientific, Logan, Utah, USA). The molar densities of CO_2 and H_2O at 64 m were measured using two independent analyzers. The first instrument was an open-path infrared gas analyzer (IRGA) mounted at a 45° angle 64 m above the ground (model LI7500; Li-Cor, Lincoln, Nebraska, USA). The second instrument was a closed-path IRGA operated in an air-conditioned hut at the base of the tower, which sampled air drawn from 64 m through 75 m of heated (65°C) 9.5 mm inner diameter Teflon PFA tube. The open-path measurement volume and closed-path air inlet were both ~0.5 m from the sonic anemometer. The closed-path gas measurements after 1 December 2000 were made by passing 22 standard L/min (slpm) through a LI7000 (Li-Cor), and, before 1 December 2000, by subsampling 8 slpm through a LI6262 (Li-Cor). The signals from the IRGAs and sonic anemometer were recorded and archived at 4 Hz. The lag-time for the closed-path IRGA was 11.75 s for CO_2 and 12.75 s for H_2O.

For the storage flux, the molar densities of CO_2 and H_2O in the profile were determined using a third IRGA.

The profile measurements were made with a LI7000 (Li-Cor) after 1 December 2000 and a LI800 (Li-Cor) prior to 1 December 2000. The IRGA sequentially sampled 12 levels between 0.1 and 64 m for 4 min each, resulting in a complete cycle every 48 min. The average CO_2 mixing ratio at each level was calculated during the last minute of each 4-min interval, and observations were then interpolated to each half-hour to synchronize with the eddy flux measurements. The amount of CO_2 stored beneath the eddy flux sensors was calculated by integrating the profile between 0 and 64 m. The storage flux was then calculated by differentiating this quantity with respect to time.

The closed-path IRGAs were calibrated automatically twice daily for CO_2 and once daily for water vapor. The gain of the open-path sensor varied little over the year, while the zero-offset drifted. We used the CO_2 and water vapor mixing ratios measured by the closed-path IRGA to calibrate the open-path IRGA CO_2 and H_2O channels.

Incoming and reflected shortwave radiation at 64 m were measured with thermopile pyranometers (model CM6B; Kipp and Zonen, Delft, The Netherlands). Net radiation at 64 m was measured with a thermopile net radiometer (model Q*7.1; REBS, Seattle, Washington, USA). Air temperatures at 64, 40, 10, and 2 m height were measured with ventilated thermistors (model 076B; Met One, Grants Pass, Oregon; model 107; Campbell Scientific, Logan, Utah, USA). Horizontal wind speed at 64, 50, and 40 m height was measured with cup anemometers (model 014; Met One).

Calculation of annual sums

Fast-response data were collected during 93% of the 17 520 half-hour intervals from 1 July 2000 to 1 July 2001. System downtime was caused by power failure

and generator or instrument maintenance. Unreliable fluxes due to equipment malfunction occurred for about 11% of the time for the open-path IRGA measurement system and 17% for the closed-path system (including calibration periods), with the longest continuous gap of 20 d caused by sonic anemometer failure. The open-path IRGA indicated window obstruction an additional ~17% of the time, mostly due to rain or dew. These intervals were discarded in subsequent analyses. Valid storage fluxes were obtained 94% of the time between 1 July 2000 and 1 July 2001.

Missing flux intervals in the yearly record were filled differently depending upon the length of the data gap and whether the gap was biased toward certain meteorological conditions. All gaps in NEE (turbulent + storage flux) shorter than 2 h were linearly interpolated between neighboring points. Longer gaps that were not biased to certain meteorological conditions were filled using mean diurnal variation (Falge et al. 2001), where the mean value for the missing half-hour interval using neighboring days was used to fill the gap. We used the 20 d of reliable data nearest the missing interval to fill the gap. Using 10 and 40 d did not appreciably change the annual sums. Missing intervals due to window obstruction of the open-path IRGA were distributed unevenly with ~20% of early morning (0100 to 0700 hours local time), 10% of late morning (0800 to 1100 hours), and 20% of afternoon (1300 to 1500 hours) intervals lost. Daytime gaps were biased toward cloudy conditions such that filling using mean diurnal variation was biased toward more sunny conditions and increased daytime CO_2 uptake. We therefore filled these gaps in NEE using a light-curve model based on this data set.

Calculation of turbulent flux

Density corrections for the open-path IRGA.—Infrared gas analyzers measure CO_2 and H_2O molar densities (ρ_c/M_c and ρ_v/M_v, respectively, in mol/m³, where ρ is mass density (g/m³) and M is molecular weight) between the source and detector. The measured CO_2 density changes both due to changing mole fraction of CO_2 and due to changes in air density caused by temperature, water vapor, and pressure. A correction is required to remove the portion of the molar density fluctuations caused by the background air density fluctuations (the WPL correction; Webb et al. 1980, Fuehrer and Friehe 2002). In the closed-path IRGA system, the sample cell pressure and temperature are constant and only water vapor effects on air density need to be considered. The open-path IRGA requires corrections for temperature and water vapor effects; pressure effects are assumed to be negligible (Webb et al. 1980).

We calculated the density corrections using two methods. The first applied the ideal gas law to each 4-Hz observation, such that the instantaneous CO_2 and H_2O mixing ratios (c and r, respectively) were calculated by dividing the measured molar densities by the instantaneous dry air molar density, ρ_a/M_a, i.e.,

$$c = \rho_c M_a/\rho_a M_c \text{ and } r = \rho_v M_a/\rho_a M_v. \quad (1)$$

The ideal gas law was used to calculate dry air density, $\rho_a = P_a/RT$, where R is the gas constant; the partial pressure of dry air, P_a, was calculated from $P_a = P - P_v$; the partial pressure of water vapor, P_v, was calculated as $P_v = (\rho_v/M_v)R_uT$, where R_u is the universal gas constant; water vapor molar density, ρ_v/M_v was returned by the open-path IRGA water vapor channel, and T was the dry air temperature, calculated by "drying" the sonic temperature (T_s) using $T \approx T_s/(1 + 0.32P_v/P)$. Because T requires the water vapor partial pressure, we first approximated $T \approx T_s$ and iterated. The turbulent flux of CO_2 was then calculated as $\overline{\rho_a c'w'}$, where the primes denote fluctuations about the mean, w is the vertical component of wind velocity, and the overbar denotes the averaging operator.

The second approach involved calculating a "raw" CO_2 flux using the measured molar density fluctuations; i.e., $\overline{(\rho_c'/M_c)w'}$, and expressing additive corrections in terms of the measured temperature and water vapor fluxes

$$F_c = \overline{\rho_c'w'} + \overline{\rho_c}\left[\frac{\mu}{\overline{\rho_a}}\overline{\rho_v'w'} + \frac{(1 + \mu\sigma)}{\overline{T}}\overline{T'w'}\right] \quad (2)$$

where $\mu = M_a/M_v$ and $\sigma = \overline{\rho_v}/\overline{\rho_a}$. Eqs. 1 and 2 are practically equivalent, requiring only that $\overline{T'^2}/\overline{T}^2 \ll 1$ and $\overline{w'T'^2}/\overline{T}^2 \ll \overline{w'T'}/\overline{T}$ (Webb et al. 1980). We determined the sensitivity of annually integrated CO_2 exchange to density correction by summing fluxes calculated with and without the correction according to both Eqs. 1 and 2.

Correction for the loss of high-frequency fluctuations when using the closed-path IRGA.—CO_2 and H_2O fluctuations at the sample inlet are damped as air travels through the tube due to longitudinal and lateral mixing, and contact with the wall (Leuning and Judd 1996). To account for these losses, we used an approach based on similarity between temperature and CO_2 and H_2O fluctuations (Goulden et al. 1996, Berger et al. 2001). The correction used a first-order filter to simulate the attenuation of fluctuations in the tubing. The time constant was found by matching power and phase spectra between temperature and CO_2 or temperature and H_2O (Shaw et al. 1998). The time constant was 0.4 s for CO_2 and 0.9 s for H_2O. We determined the sensitivity of annually integrated CO_2 exchange to the high-frequency correction by summing fluxes calculated both with and without the correction.

Averaging time and detrending.—Recent discussion has focused on the possibility that low-frequency contributions to fluxes are underestimated when insufficient averaging times are used (Sakai et al. 2001, Finnigan et al. 2003). An underestimation of low-fre-

quency flux may also result from linear detrending, which is commonly applied before calculating covariances. We determined the sensitivity of annually integrated CO_2 exchange to these low frequency motions by summing fluxes calculated (1) using averaging times of 30 min and 2 h, and (2) both with and without linear detrending.

Treatment of calm periods.—The integration of tower-based estimates of NEE to obtain annual sums is particularly sensitive to day-to-night measurement biases (Goulden et al. 1996). Atmospheric mixing changes markedly from day to night with surface heating and cooling. The formation of a stable boundary layer on calm nights may result in the removal of CO_2 from a site by mechanisms that are not measured by the eddy covariance technique (Fitzjarrald and Moore 1990, Lee 1998). Biological CO_2 production at night is expected to be independent of above-canopy turbulent mixing (Goulden et al. 1996). Evidence for the loss of CO_2 on calm nights is provided by plots showing a reduction in NEE during calm nights. The ''$u*$ filter'' method replaces nocturnal NEE during weakly mixed periods with a value measured during well-mixed conditions ($u*$ refers to the friction velocity; see Goulden et al. [1996*b*] for details). However, the use of a $u*$ filter, and the appropriate threshold, have not been uniformly agreed upon by the research community. We determined the sensitivity of annually integrated CO_2 exchange to the $u*$ filter by summing fluxes with and without the correction, and with various $u*$ thresholds.

The data reported in this paper are available online.[4,5]

RESULTS

Biometric measurements of carbon balance

Measurements of biomass, and the change in biomass with time, provide a much-needed bound on the plausible rates of carbon sequestration by an ecosystem. In the event of a ''large net carbon sink in the undisturbed rain forest'' (Andreae et al. 2002), we would expect to see a significant increase in forest biomass over time.

We used data from three inventories of forest biomass over a 16-yr period to calculate the annual carbon balance (Table 1). An average of 22 trees per hectare with dbh > 55 cm were found in the 48-ha area of block 10b during the 1984 IBAMA survey (Table 1). Likewise, an average of 21 trees per hectare were found in block 10b during the 2000 TREVISO survey. The corresponding aboveground biomass for large trees was 84 Mg C/ha for the 1984 IBAMA survey and 78 Mg C/ha for the 2000 TREVISO survey (Table 1), indicating that there was no accumulation of carbon in large trees during this period. The total AGLB was 197 Mg C/ha for the 1984 IBAMA survey and 185 Mg C/ha

for the 2000 TREVISO survey (Table 1), indicating a net rate of loss of carbon during this period of 0.8 ± 1.5 Mg C·ha^{-1}·yr^{-1} (see *Methods* for discussion of uncertainty).

Soil can also store carbon. Malhi et al. (1999) suggested tropical soils may be a large carbon sink (-3.6 Mg C·ha^{-1}·yr^{-1}) based on the high annual ecosystem uptake measured using eddy covariance. However, we are unaware of any direct geochemical evidence supporting this claim. Trumbore et al. (1995; S. E. Trumbore, *personal communication*) used carbon isotopes and measurements of carbon stocks to conclude that the capacity of undisturbed tropical forest soil to store carbon is 0 ± 0.5 Mg C·ha^{-1}·yr^{-1}.

The biometric results therefore indicate the carbon balance from 1984 to 2000 was +0.8 ± 2 Mg C·ha^{-1}·yr^{-1}. We emphasize that this uncertainty is conservative. The IBAMA and TREVISO surveys indicate that the number of large trees decreased slightly or remained constant from 1984 to 2000, and it is unlikely that there was appreciable carbon accumulation in large trees (Table 1). Moreover, there is no specific reason to believe that tree demography changed between surveys or that the soil was perturbed from steady state. In conclusion, we did not find any biometric evidence of rapid carbon accumulation by the forest, and believe the net carbon accumulation from 1984 to 2000 was close to zero.

Meteorology and forest seasonality

Air temperature was relatively constant year-round, allowing a 12-mo growing season and a high gross primary production ($\sim$30 Mg C·ha^{-1}·yr^{-1}). Total rainfall was over 2000 mm from 1 July 2000 to 1 July 2001, with most occurring in the wet season from December to June (Fig. 2a). Average rainfall was 1889 mm/yr for 1986–1999 based on the Global Precipitation Climate Center (GPCC) database, and 1998 mm/yr for 1 January 1998 to 1 January 2000 based on TRMM satellite data (Huffman 1995), implying that 1 July 2000 to 1 July 2001 was somewhat wetter than average. The wind at 64 m was generally from the east at 2 to 4 m/s (Fig. 2b, c). The wind occasionally shifted to westerly during the afternoon as a result of a river circulation caused by the Tapajós River. Daytime was characterized by strong convective mixing and nights were calm and stably stratified, with a reduction in vertical turbulent exchange.

While the incoming radiation at the top of the atmosphere was relatively constant year-round (varied about 12%), the net radiation balance above the forest varied seasonally in response to increased wet-season cloudiness (da Rocha et al. 2004). Net radiation during daytime was lower and more variable during the wet season, resulting in more variable fluxes of momentum, heat, moisture, and CO_2 (Fig. 2b). Net radiation during nighttime was less negative during the wet season due
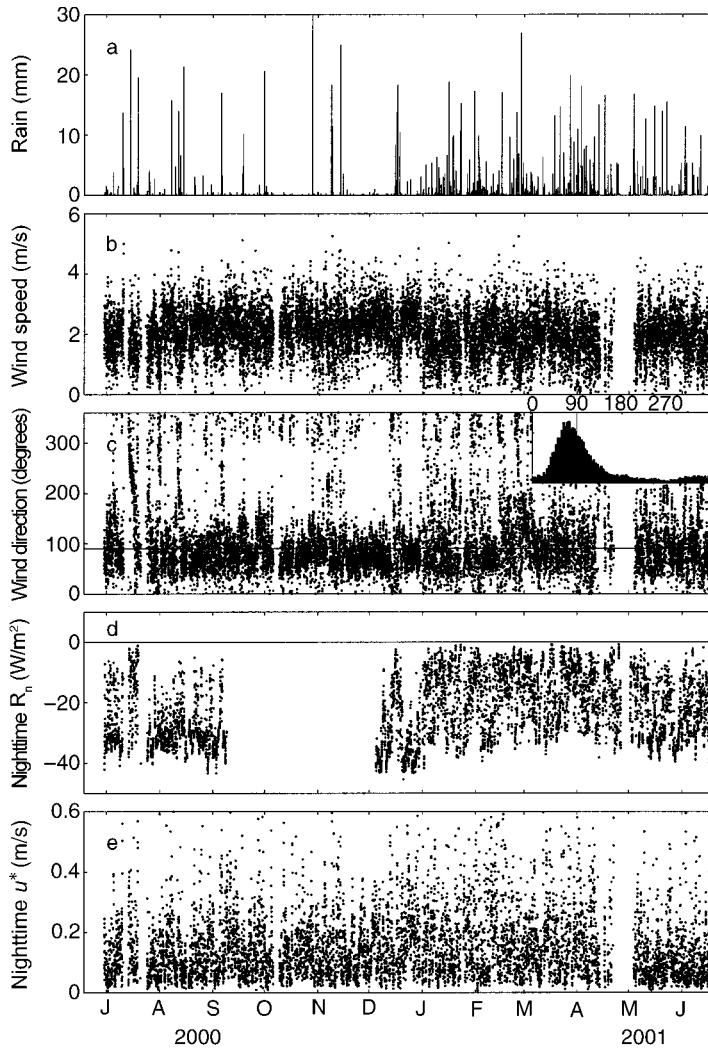
FIG. 2. Half-hourly meteorological variables measured at 64 m at Flona Tapajós, km 83, from 1 July 2000 to 1 July 2001: (a) rainfall (mm), (b) wind speed (m/s), (c) wind direction in meteorological convention (inset shows histogram of half-hourly mean wind direction), (d) nighttime net radiation (W/m²); missing interval due to degraded sensor performance), and (e) nighttime friction velocity, $u* = (-\overline{u'w'})^{1/2}$ (m/s).

to increased downward longwave energy (Fig. 2d). The nocturnal sky was comparatively clear during the dry season, causing increased canopy cooling, more stable conditions, and reduced vertical mixing. Friction velocity was below 0.2 m/s during 70% of the nighttime intervals in the wet season and 77% of the nighttime intervals in the dry season (Fig. 2e).

Average peak daytime CO_2 uptake was ~16 μmol·m^{-2}·s^{-1}, and measured nocturnal CO_2 efflux was ~5 μmol·m^{-2}·s^{-1} (Fig. 3b, c). The turbulent and storage fluxes of CO_2 were of comparable magnitude, as stable nighttime conditions resulted in large CO_2 accumulation within the nocturnal boundary layer. The CO_2 concentration at 64 m had an average maximum nighttime value of 400 ppm, with occasional peaks of 440 ppm. Relatively high rates of daytime uptake occurred during the dry season due to increased canopy activity (Goulden et al. 2004). Relatively high rates of nighttime respiration occurred during the wet season.

Tower-based measurement of carbon balance

Cumulative sums of calculated carbon exchange are shown in Fig. 4 for 12 different hardware configurations and data treatments. The different combinations yielded annual sums that ranged from a large carbon sink to a small carbon source. The annual sum obtained by integrating NEE (turbulent flux plus storage flux) calculated using the closed-path IRGA, 30-min averaging, no detrending, and high-frequency corrections for tubing attenuation, was −3.9 Mg C·ha^{-1}·yr^{-1} (Fig. 4, curve 1, referred to as the baseline sum). This methodology is similar to that used during previous work in Amazonia, including Grace et al. (1995), who reported an annual sum of −1.0 Mg C·ha^{-1}·yr^{-1}, and Malhi et al. (1998), who reported an annual sum of −5.9 Mg C·ha^{-1}·yr^{-1}. Although no two sites are identical, our baseline sum is consistent with the reports by Grace et al. (1995), Malhi et al. (1998), Andreae et al. (2002), and Araújo et al. (2002).

FIG. 3.   CO$_2$ fluxes at Flona Tapajós, km 83, from 1 July 2000 to 1 July 2001: (a) fraction of missing turbulent flux intervals for open (solid) and closed (dashed) path systems (one value is given for each day, and the curve is smoothed by averaging over 10 d surrounding the interval), (b) half-hourly turbulent CO$_2$ flux (F_c; μmol·m^{-2}·s^{-1}) from the closed-path system, and (c) half-hourly CO$_2$ storage flux (F_s; μmol·m^{-2}·s^{-1}) from the CO$_2$ profile measured between 0 and 64 m.
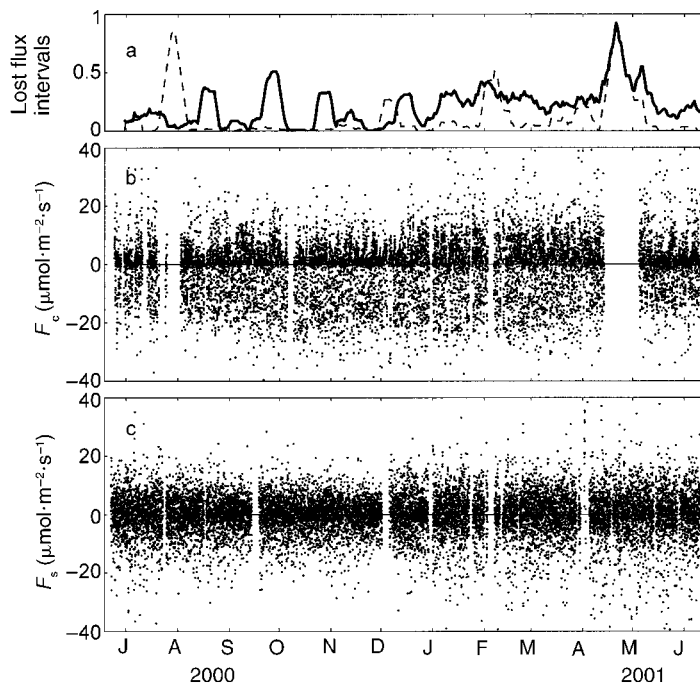
Density and frequency corrections; comparison between open- and closed-path analyzers

The high-frequency correction for the closed-path system changed the annual sum by 0.3 Mg C·ha^{-1}·yr^{-1} (Fig. 4, curve 2 relative to 1). The correction increased the flux magnitude by 1.5% (-0.2 μmol·m^{-2}·s^{-1}) during daytime and 8% (0.2 μmol·m^{-2}·s^{-1}) during nighttime (Fig. 5a, b). Nocturnal CO$_2$ spectra indicate the tubing attenuates the amplitude of fluctuations for frequencies above 0.2 Hz (Fig. 6a). If the tubing is described by a first-order low-pass filter (see *Methods*) the phase spectrum will be distorted at frequencies lower than 0.2 Hz. However, the nighttime wc co-spectrum showed little high-frequency attenuation (Fig. 6b), and, hence, the frequency corrections were small.

Curves 8 (no WPL correction) and 9 (the result of a bias in gap filling of the open-path IRGA during rainy intervals) in Fig. 4 indicate the magnitude of underlying corrections, and are not intended as accurate measures of integrated flux. The density, or WPL, correction for the open-path sensor changed the annual sum by 4.5 Mg C·ha^{-1}·yr^{-1} (Fig. 4, curve 7 relative to 9), reducing the ''raw'' flux magnitude by 30–35% (5–7 μmol·m^{-2}·s^{-1}) during convective daytime conditions and 15% (-0.4 μmol·m^{-2}·s^{-1}) during stable nighttime conditions (Fig. 5a, b). A regression between the CO$_2$ fluxes calculated with Eqs. 1 and 2 showed excellent agreement ($F_c^{eq2} = 0.99 F_c^{eq1} + 0.07$, $r^2 = 1$, $n = 13\,428$, where F_c indicates turbulent CO$_2$ flux [μmol·m^{-1}·s^{-1}], and superscripts ''eq 1'' and ''eq 2'' indicate whether the WPL correction was applied using Eq. 1 or Eq. 2). The correction using Eq. 1 resulted in about 1.5%

(-0.25 μmol·m^{-2}·s^{-1}) higher peak daytime uptake. This difference resulted in a change in annual exchange of 0.5 Mg C·ha^{-1}·yr^{-1} (Fig. 4, curve 10 relative to 7).

The method used to gap fill the open-path fluxes resulted in a large change in the annual sum (2.1 Mg C·ha^{-1}·yr^{-1}, Fig. 4, curve 8 relative to curve 10). The frequent precipitation resulted in a large number of missing intervals for the open-path IRGA, especially during the rainy season (Fig. 3a). These missing intervals were inversely related with sunlight, resulting in a bias if they were not filled correctly (Fig. 4, curve 8). We gap filled NEE for the open-path using a light-curve model based on the current dataset to compensate for the below-average sunlight during missing intervals (Fig. 4, curve 10).

The accuracy of fluxes from open path IRGAs is often criticized based on the magnitude of the WPL correction (Fig. 5). However, we found that a well-calibrated open-path IRGA combined with the WPL correction and a light-curve model to gap-fill biased rainy intervals provided good agreement with the closed-path system (difference of 1.1 Mg C·ha^{-1}·yr^{-1}; Fig. 4, curve 1 relative to curves 10 or 7, and Figs. 6 and 7). The regression of individual fluxes between open- and closed-path systems had a slope within 5% of unity and an R^2 of 0.9. The 20% increase in integrated carbon uptake calculated from the open-path system is attributed to the regression offset of -0.23 μmol·m^{-2}·s^{-1}, equivalent to ~1 Mg C·ha^{-1}·yr^{-1}.

Averaging time and detrending

Energy budget closure is often used as a metric for assessing whether daytime turbulent fluxes are under-
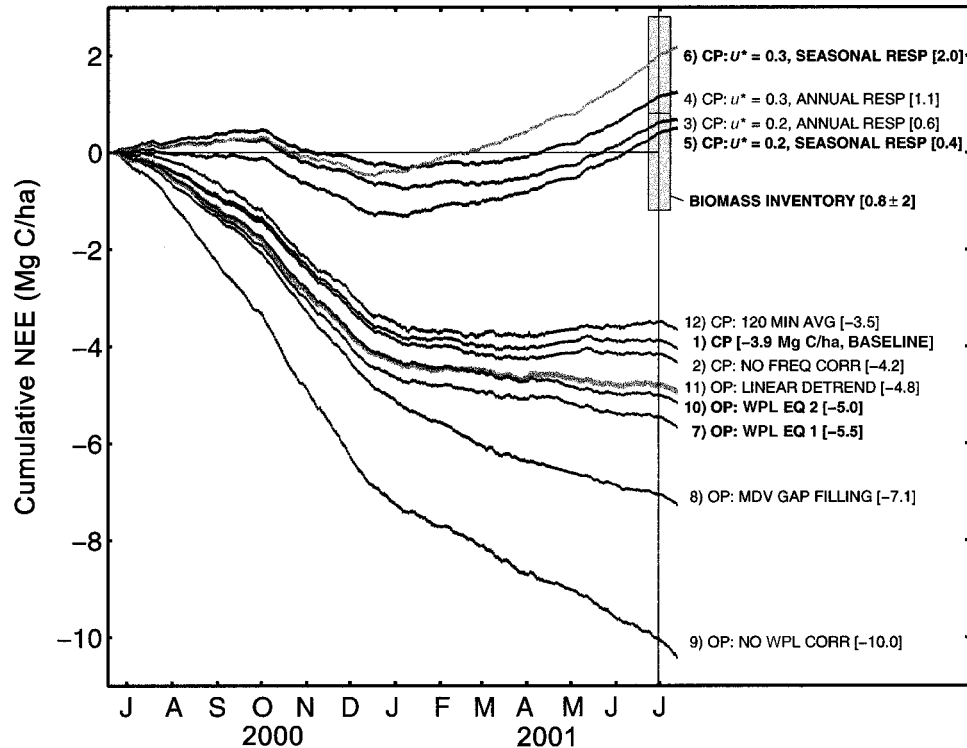
FIG. 4. Cumulative NEE (turbulent flux + storage flux) from July 2000 to July 2001 at Flona Tapajós, km 83 (Mg C/ha). All curves are based on a 30-min flux calculation interval except where noted. Net carbon exchanges between 1 July 2000 and 1 July 2001 (Mg C/ha) are shown in square brackets. Boldface labels indicate plausible scenarios, as discussed in *Results*. Key: curve 1, closed-path IRGA with high-frequency correction; curve 2, closed-path IRGA with no high-frequency correction; curve 3, closed-path IRGA with high-frequency correction and a nighttime $u*$ correction based on the annually averaged respiration (Fig. 8) with threshold $u* = 0.2$ m/s; curve 4, same as curve 3, except threshold $u* = 0.3$ m/s; curve 5, closed-path IRGA with high-frequency correction and a nighttime $u*$ correction based on the seasonal course of respiration (see Goulden et al. 2004) with threshold $u* = 0.2$ m/s; curve 6, same as curve 5, except $u* = 0.3$ m/s; curve 7, open-path IRGA with WPL correction based on Eq. 1 and daytime gaps filled using a light-curve model, NEE = 6.5 + (−39.5PPFD)/(907 + PPFD); curve 8, same as curve 7, except daytime gaps filled by mean diurnal variation (Falge et al. 2001) instead of the light-curve model; curve 9, open-path IRGA without WPL corrections, with daytime gaps filled using the light-curve model; curve 10, same as curve 7 except WPL correction applied using Eq. 2; curve 11, same as curve 10, except vertical velocity and CO_2 mole fraction time series linearly detrended before calculating fluxes; curve 12, same as curve 1, except 120-min averaging interval used to calculate fluxes.

estimated. The overall closure for this data set was 87%, taking into account net radiation, sensible and latent heat fluxes, and biomass, soil, and canopy storage fluxes (da Rocha et al. 2004). Increasing the averaging time to 2 h did not appreciably improve the closure of the energy budget (plot not shown), suggesting the 30-min averaging time is sufficient. The 2-h averaging time resulted in an annual CO_2 exchange of −3.5 Mg C·ha^{-1}·yr^{-1}, which is 10–15% less negative than the baseline sum (Fig. 4, curve 12 relative to curve 1). This implies that the underestimation of low-frequency CO_2 flux had a greater effect at night.

Linear detrending reduced the 30-min averaged fluxes for the open-path IRGA by only 0.4% during daytime and 0.3% at night, corresponding to an annual sum difference of 0.2 Mg C·ha^{-1}·yr^{-1} (Fig. 4, curve 11 relative to curve 10). We conclude that the underesti-

mation of low-frequency flux has a modest effect on the calculated annual sum.

Treatment of calm nights

We found a dependence of nighttime exchange (NEE) on above-canopy turbulent mixing. Fig. 8 indicates that nighttime NEE was reduced at $u* < 0.2$ m/s. However, automated chamber measurements at the site indicated that CO_2 efflux from the soil was not suppressed at low $u*$ (plot not shown; see Goulden et al. 2004). Moreover, biological production of CO_2 by plant and microbial respiration is generally considered to be independent of above-canopy turbulent mixing. Consequently, we believe the reduction in NEE on calm nights results from the transport of CO_2 from the forest by mechanisms not measured by eddy covariance (Goulden et al. 1996). Independent measurements in
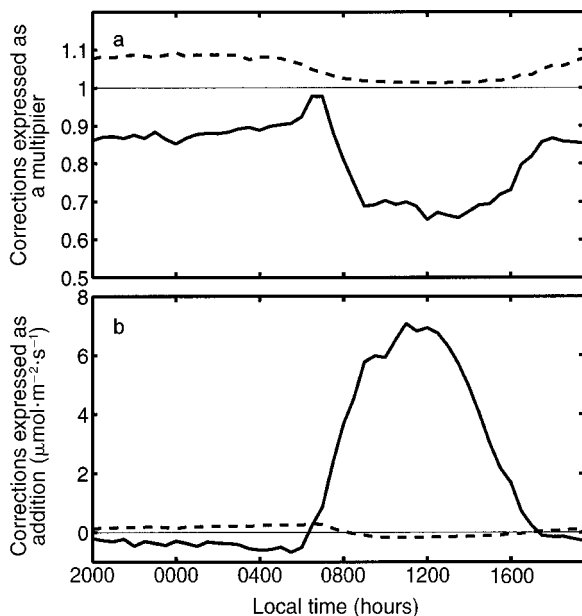
FIG. 5. Average daily course of density (WPL) corrections for the open-path system (solid line), and high-frequency attenuation corrections for the closed-path system (dashed line), from July 2000 to July 2001. Raw flux is $\overline{\rho_c' w'}$ using the CO_2 density that is returned by the IRGA. (a) Corrections expressed as a multiplier to the "raw" CO_2 flux from the instrument. (b) Corrections expressed as an additive correction to the "raw" CO_2 flux ($\mu mol \cdot m^{-2} \cdot s^{-1}$).

Amazonia support the interpretation that NEE measured using micrometeorology underestimates biotic CO_2 production on calm nights. Boundary layer CO_2 budgets in Rondônia by Culf et al. (1997) indicated that the CO_2 efflux measured using eddy covariance during calm nights underestimated the regional CO_2 efflux. Chambers et al. (2004) estimated ecosystem respiration from soil, stem, and leaf respiration measurements in a forest near Manaus, and obtained an average ecosystem respiration of 8.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$, consistent with our nighttime NEE value during well-mixed periods (Fig. 8).

Applying the $u*$ filter had a dramatic effect on the annual sum. A $u*$ threshold of 0.2 m/s resulted in an annual sum of +0.6 Mg C·ha^{-1}·yr^{-1} (a source of carbon) and a threshold of 0.3 m/s resulted in an annual sum of +1.1 Mg C·ha^{-1}·yr^{-1} (Fig. 4, curves 4 and 3 relative to curve 1). Malhi et al. (1998) and Araújo et al. (2002) measured a similar dependence of nighttime NEE on $u*$ above forest near Manaus. Malhi et al. (1998) attributed this pattern to an underestimation of the storage flux, and argued against applying a correction for nighttime NEE underestimation. Grace et al. (1996) and Kruijt et al. (2004) found no reduction in NEE during calm nighttime conditions at a Rondônia site, underlining the uncertainty over the need to apply a $u*$ filter.

We found that nocturnal NEE varied seasonally, with respiration rates ~2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ higher during the wet
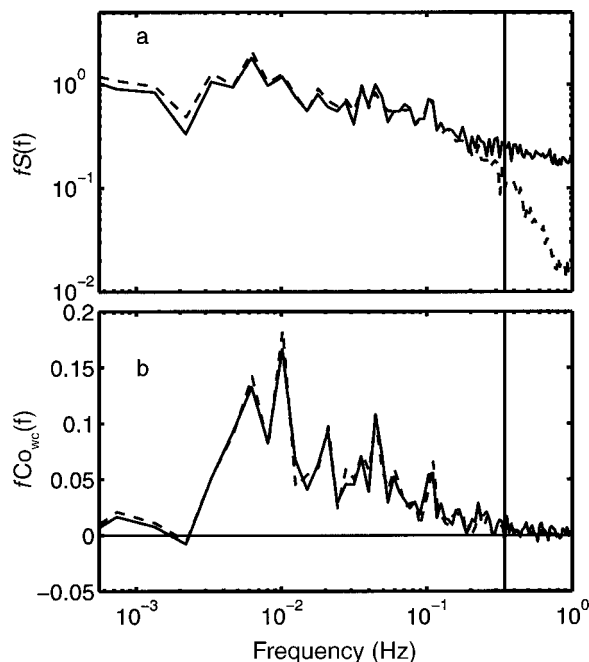

FIG. 6. Nighttime frequency response of open- and closed-path systems measured on 12 January 2001, 0330 hours local time. Mean wind speed at 64 m was 1.8 m/s. (a) Frequency (f; Hz)-weighted power spectra (S; [ppm]^2/Hz) of CO_2 mixing ratio for open (solid) and closed (dashed) path IRGAs. (b) Frequency-weighted co-spectrum (Co$_{wc}$; μmol $CO_2 \cdot m^{-2} \cdot s^{-1} \cdot Hz^{-1}$) between vertical velocity and CO_2 mixing ratio for open- and closed-path IRGAs. The vertical lines are at 0.2 Hz.

season (Goulden et al. 2004). Nocturnal $u*$ was also slightly higher in the wet season (Fig. 2e), creating a bias if low-respiration dry season nights were filled with an annual mean that is weighted toward high-
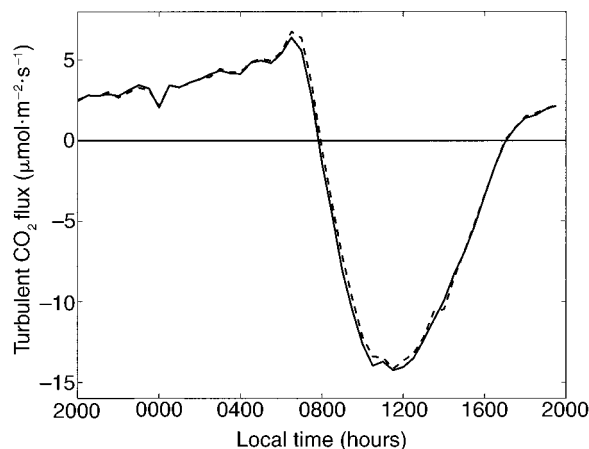

FIG. 7. Daily cycle of turbulent CO_2 flux from open (solid) and closed (dashed) path IRGAs. Each curve contains 48 points, one for each half-hour daily interval. Each point is the average flux of all reliable fluxes for that interval over the year.
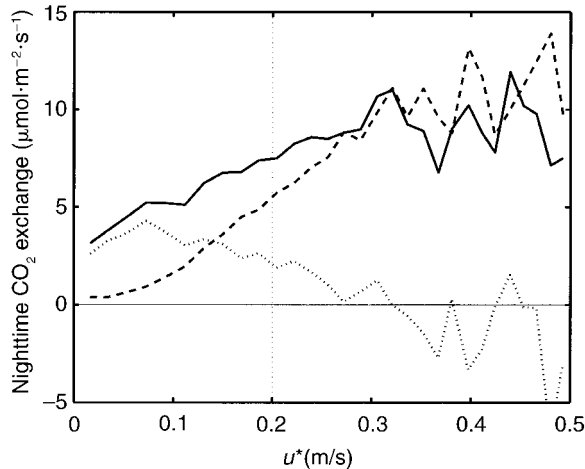
FIG. 8. Nighttime CO_2 exchange ($\mu mol \cdot m^{-2} \cdot s^{-1}$) vs. friction velocity (m/s): turbulent CO_2 flux (dashed), CO_2 storage in air column between 0 and 64 m (dotted), and their sum (NEE) (solid). The vertical line corresponds to $u^* = 0.2$ m/s.
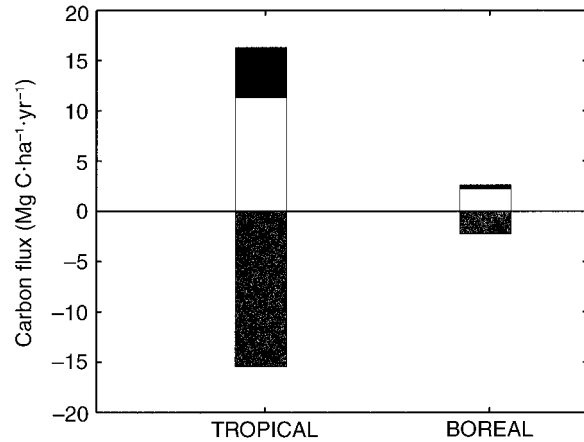

FIG. 9. Effect of nighttime uncertainty on annualized sums of tower-based ecosystem exchange for the tropical forest reported here and the BOREAS NOBS site, a boreal forest in Canada (from Goulden et al. 1997). Annual daytime carbon uptake (gray), annual nighttime carbon efflux not corrected for u^* (clear), and annual nighttime correction with $u^* = 0.2$ m/s (black).

respiration wet season observations. Hence, we applied the u^* filter using a seasonally varying rate of respiration (see Goulden et al. 2004). This approach resulted in annual sums of +0.4 Mg C·ha^{-1}·yr^{-1} for a u^* threshold of 0.2 m/s and +2.0 for a u^* threshold of 0.3 m/s (Fig. 4, curves 5 and 6 relative to curve 1).

DISCUSSION

Which annual sum is correct?

The biometry-based carbon balance indicated there was no accumulation in large trees, which represent a significant portion of AGLB. The inventories established that the forest was either a source or, at most, a modest sink of carbon from 1984 to 2000 (+0.8 ± 2 Mg C·ha^{-1}·yr^{-1}). Based on the evidence that NEE is underestimated during calm nights (Fig. 8), we believe that curve 5 (+0.4 Mg C·ha^{-1}·yr^{-1}) provides our best estimate of the tower-based annual carbon balance, and that the forest was approximately carbon neutral from July 2000 to July 2001. This result is consistent with the biomass inventories, providing further evidence that the forest was not a large carbon sink during the study.

Is uncertainty in tower-based carbon balance greater for tropical than temperate forest?

There is a widespread assumption that tower-based carbon balances for tropical forest are just as reliable as those for temperate forest. However, the sensitivity analysis revealed that the uncertainty of the annual sum for this tropical forest is much larger than we had expected based on previous work in mid- and high-latitude forest (Fig. 4; Goulden et al. 1996, 1997). The use of micrometeorology to determine the carbon balance of evergreen tropical forest suffers from a simple weakness. Evergreen tropical forest has a high rate of

respiration year-round, which causes a large annual nocturnal efflux. In turn, this increases the effect of the u^* filter on the calculation of the annual net flux, which decreases confidence in the tower-based NEP.

The main cause of uncertainty at the tropical site is the very large effect of the u^* filter on calculated annual exchange. The effect of the u^* filter was five to 10 times greater at the tropical site than has been previously reported for sites in Canada (Fig. 9; Goulden et al. 1997) and Massachusetts (Fig. 10; Barford et al. 2001). The site-to-site differences in sensitivity to the u^* filter are related to site-to-site differences in the
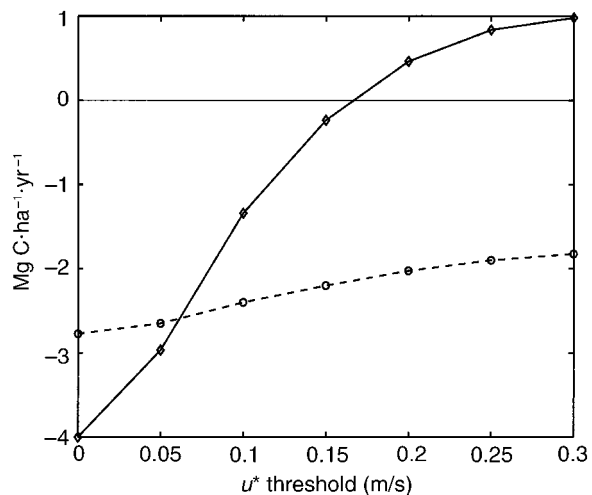

FIG. 10. The effect of filtering threshold on the annually integrated carbon exchange for the tropical forest reported here (solid line with diamonds) and Harvard Forest, a deciduous forest in Massachusetts (dashed line with circles; from Barford et al. 2001).

magnitude of annually integrated nocturnal CO_2 exchange. The annual nocturnal flux was relatively small in the boreal forest, since the growing season was brief and the summer nights were short (Fig. 9). In contrast, the annual nocturnal flux was large in the tropical forest, since high rates of respiration continued year-round. The effect of the $u*$ filter was roughly proportional to the annual nocturnal flux, and consequently the $u*$ filter caused a much greater change in the annual sum at the tropical site than the temperate sites. We believe Fig. 8 provides strong evidence for the need to correct the annual sum using a $u*$ filter. At the same time, we concede that the $u*$ filter introduces uncertainty into the annual sum, and that this uncertainty is proportional to the magnitude of the correction.

The best approach for treating nocturnal flux is not agreed upon within the meteorological community, resulting in dramatically divergent reports of annual CO_2 exchange. Past reports of large carbon uptake by old growth Amazonian forest are largely attributable to decisions not to correct for calm nights when calculating annual sums (Malhi et al. 1998, Andreae et al. 2002). Our comparison between tower-based and biometry-based annual sums reinforces the importance of independent measurements of NEP to obtain accurate annual sums in tropical forest. Our tower flux result considered in isolation does not provide *strong* evidence that the forest was carbon neutral during the study, since there was a large uncertainty associated with the $u*$ correction. However, the biometric and micrometeorological measurements reinforce each other, and taken in combination, provide strong evidence that our site was not a strong carbon sink during the study interval.

Literature Cited

Andreae, M. O., et al. 2002. Biogeochemical cycling of carbon, water, energy, trace gases, and aerosols in Amazonia: the LBA-EUSTACH experiments. Journal of Geophysical Research-Atmospheres **107**(D20):8066.

Araújo, A. C., A. D. Nobre, B. Kruijt, J. Elbers, R. Dallarosa, P. Stefani, C. Randow, A. O. Manzi, A. D. Culf, and J. H. C. Gash. 2002. Comparative measurements of carbon dioxide fluxes from two nearby towers in a central Amazonian rain forest: the Manaus LBA site. Journal of Geophysical Research-Atmospheres **107**(D20):8090.

Aubinet, M., et al. 2000. Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. Advances in Ecological Research **30**:13–175.

Baldocchi, D. D., B. B. Hicks, and T. P. Meyers. 1988. Measuring biosphere–atmosphere exchanges of biologically related gases with micrometeorological methods. Ecology **69**: 1331–1340.

Barford, C. C., S. C. Wofsy, M. L. Goulden, J. W. Munger, E. H. Pyle, S. P. Urbanski, L. Hutyra, S. R. Saleska, D. Fitzjarrald, and K. Moore. 2001. Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. Science **294**:1688–1691.

Berger, B. W., K. J. Davis, C. Yi, P. S. Bakwin, and C. L. Zhao. 2001. Long-term carbon dioxide fluxes from a very tall tower in a northern forest: flux measurement methodology. Journal of Atmospheric and Oceanic Technology **18**: 529–542.

Chambers, J. Q., J. P. Schimel, and A. D. Nobre. 2001. Respiration from coarse wood litter in central Amazon forests. Biogeochemistry **52**:115–131.

Chambers, J. Q., E. S. Tribuzy, L. C. Toledo, B. F. Crispim, N. Higuchi, J. dos Santos, A. C. Araújo, B. Kruijt, A. D. Nobre, and S. E. Trumbore. 2004. Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. Ecological Applications **14**:S72–S88.

Culf, A. D., G. Fisch, Y. Malhi, and C. A. Nobre. 1997. The influence of the atmospheric boundary layer on carbon dioxide concentrations over a tropical forest. Agricultural and Forest Meteorology **85**(N3):149–158.

da Rocha, H. R., M. L. Goulden, S. D. Miller, M. C. Menton, L. D. V. O. Pinto, H. C. de Freitas, and A. M. e Silva Figueira. 2004. Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia. Ecological Applications **14**:S22–S32.

Falge, E., et al. 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. Agricultural and Forest Meteorology **107**:43–69.

Finnigan, J. J., R. Clement, Y. Malhi, R. Leuning, and H. A. Cleugh. 2003. A re-evaluation of long-term flux measurement techniques. Part I: averaging and coordinate rotation. Boundary Layer Meteorology **107**:1–48.

Fitzjarrald, D. R., and K. Moore. 1990. Mechanisms of nocturnal exchange between the rainforest and the atmosphere. Journal of Geophysical Research-Atmospheres **95**(D10):16 839–16 850.

Fuehrer, P. L., and C. A. Friehe. 2002. Flux corrections revisited. Boundary-Layer Meteorology **102**(N3):415–458.

Goulden, M. L., B. C. Daube, S. M. Fan, D. J. Sutton, A. Bazzaz, J. W. Munger, and S. C. Wofsy. 1997. Physiological responses of a black spruce forest to weather. Journal of Geophysical Research-Atmospheres **102**:28 987–28 996.

Goulden, M. L., S. D. Miller, H. R. da Rocha, M. C. Menton, H. C. de Freitas, A. M. e Silva Figueira, and C. A. Dias de Sousa. 2004. Diel and seasonal patterns of tropical forest CO_2 exchange. Ecological Applications **14**:S42–S54.

Goulden, M. L., J. W. Munger, S.-M. Fan, B. C. Daube, and S. C. Wofsy. 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Global Change Biology **2**:169–182.

Grace, J., J. Lloyd, J. Mcintyre, A. C. Miranda, P. Meir, H. S. Miranda, C. Nobre, J. Moncrieff, J. Massheder, Y. Malhi, I. Wright, and J. Gash. 1995. Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia. Science **270**:778–780.

Grace, J., Y. Malhi, J. Lloyd, J. McIntyre, A. C. Miranda, P. Meir, and H. S. Miranda. 1996. The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. Global Change Biology **2**:208–217.

Hernandez Filho, P., Y. E. Shimabukuro, and D. C. L. Lee. 1993. Final report on the forest inventory project at the

Tapajós National Forest. Instituto Nacional de Pesquisas Espaciais, São José dos Campos, SP, Brasil.

Huffman, G. J., R. F. Adler, B. Rudolph, U. Schneider, and P. Keehn. 1995. Global precipitation estimates based on a technique for combining satellite-based estimates, rain gauge analysis, and NWP model precipitation information. Journal of Climate **8**:1284–1295.

Keller, M., M. Palace, and G. Hurtt. 2001. Biomass estimation in the Tapajós National Forest, Brazil. Examination of sampling and allometric uncertainties. Forest Ecology and Management **154**:371–382.

Kruijt, B., J. A. Elbers, C. von Randow, A. C. Araújo, P. J. Oliveira, A. Culf, A. O. Manzi, A. D. Nobre, P. Kabat, and E. J. Moors. 2004. The robustness of eddy correlation fluxes for Amazon rain forest conditions. Ecological Applications **14**:S101–S113.

Lee, X. 1998. On micrometeorological observations of surface–air exchange over tall vegetation. Agricultural and Forest Meteorology **91**:39–49.

Leuning, R., and M. J. Judd. 1996. The relative merits of open- and closed-path analysers for measurements of eddy fluxes. Global Change Biology **2**:241–253.

Malhi, Y., D. D. Baldocchi, and P. G. Jarvis. 1999. The carbon balance of tropical, temperate and boreal forests. Plant, Cell and Environment **22**:715–740.

Malhi, Y., A. D. Nobre, J. Grace, B. Kruijt, M. G. P. Pereira, A. Culf, and S. Scott. 1998. Carbon dioxide transfer over a Central Amazonian rain forest. Journal of Geophysical Research-Atmospheres **103**:31 593–31 612.

Moncrieff, J. B., Y. Malhi, and R. Leuning. 1996. The propagation of errors in long-term measurements of land–atmosphere fluxes of carbon and water. Global Change Biology **2**:231–240.

Phillips, O. L., Y. Malhi, N. Higuchi, W. F. Laurance, P. V. Nunez, R. M. Vasquez, S. G. Laurance, L. V. Ferreira, M. S. Stern, S. Brown, and J. Grace. 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. Science **282**:439–442.

Phillips, O. L., et al. 2002. Increasing dominance of large lianas in Amazonian forests. Nature **418**:770–774.

Sakai, R. K., D. R. Fitzjarrald, and K. E. Moore. 2001. Importance of low-frequency contributions to eddy fluxes observed over rough surfaces. Journal of Applied Meteorology **40**:2178–2191.

Shaw, W. J., C. W. Spicer, and D. V. Kenny. 1998. Eddy correlation fluxes of trace gases using a tandem mass spectrometer. Atmospheric Environment **32**(17):2887–2898.

Trumbore, S. E., E. A. Davidson, P. B. de Camargo, D. C. Nepsted, and L. A. Martinelli. 1995. Belowground cycling of carbon in forests and pastures of Eastern Amazonia. Global Biogeochemical Cycles **9**(4):515–528.

Valentini, R., et al. 2000. Respiration as the main determinant of carbon balance in European forests. Nature **404**:861–865.

Waring, R. H., and W. Schlesinger. 1985. Forest ecosystems: concepts and management. Academic Press, Orlando, Florida, USA.

Watson, R. T., editor. 2000. Land use, land-use change, and forestry: a special report of the IPCC. Intergovernmental Panel on Climate Change (IPCC), Cambridge University Press, Cambridge, UK.

Webb, E. K., G. I. Pearman, and R. Leuning. 1980. Correction of flux measurements for density effects due to heat and water vapor transfer. Quarterly Journal Royal Meteorological Society **106**:85–100.

Wofsy, S. C., M. L. Goulden, J. W. Munger, S. M. Fan, P. S. Bakwin, B. C. Daube, S. L. Bassow, and F. A. Bazzaz. 1993. Net exchange of CO_2 in a mid-latitude forest. Science **260**:1314–1317.