

CARBON BALANCE AND VEGETATION DYNAMICS IN AN OLD-GROWTH AMAZONIAN FOREST

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Abstract. Amazon forests could be globally significant sinks or sources for atmospheric carbon dioxide, but carbon balance of these forests remains poorly quantified. We surveyed 19.75 ha along four 1-km transects of well-drained old-growth upland forest in the Tapajós National Forest near Santarém, Pará, Brazil (2°51' S, 54°58' W) in order to assess carbon pool sizes, fluxes, and climatic controls on carbon balance. In 1999 there were, on average, 470 live trees per hectare with diameter at breast height (dbh) ≥ 10 cm. The mean (and 95% CI) aboveground live biomass was 143.7 ± 5.4 Mg C/ha, with an additional 48.0 ± 5.2 Mg C/ha of coarse woody debris (CWD). The increase of live wood biomass after two years was 1.40 ± 0.62 Mg C·ha⁻¹·yr⁻¹, the net result of growth (3.18 ± 0.20 Mg C·ha⁻¹·yr⁻¹ from mean bole increment of 0.36 cm/yr), recruitment of new trees (0.63 ± 0.09 Mg C·ha⁻¹·yr⁻¹, reflecting a notably high stem recruitment rate of $4.8 \pm 0.9\%$), and mortality (-2.41 ± 0.53 Mg C·ha⁻¹·yr⁻¹ from stem death of 1.7% yr⁻¹). The gain in live wood biomass was exceeded by respiration losses from CWD, resulting in an overall estimated net loss from total aboveground biomass of 1.9 ± 1.0 Mg C·ha⁻¹·yr⁻¹. The presence of large CWD pools, high recruitment rate, and net accumulation of small-tree biomass, suggest that a period of high mortality preceded the initiation of this study, possibly triggered by the strong El Niño Southern Oscillation events of the 1990s. Transfer of carbon between live and dead biomass pools appears to have led to substantial increases in the pool of CWD, causing the observed net carbon release. The data show that biometric studies of tropical forests neglecting CWD are unlikely to accurately determine carbon balance. Furthermore, the hypothesized sequestration flux from CO₂ fertilization (<0.5 Mg C·ha⁻¹·yr⁻¹) would be comparatively small and masked for considerable periods by climate-driven shifts in forest structure and associated carbon balance in tropical forests.

Key words: biometry; carbon balance; carbon release; carbon sequestration; coarse woody debris; El Niño; LBA; mortality; tropical forest.

INTRODUCTION

In recent years, about one half of anthropogenic carbon dioxide emissions have remained in the atmosphere, while oceans and the terrestrial biosphere have taken up the balance (Dixon et al. 1994, Schimel 1995, Prentice et al. 2001). The mechanisms and location of the terrestrial sink for atmospheric carbon dioxide remain controversial. Model studies constrained by global atmospheric measurements tend to place the terrestrial sink in the northern midlatitudes (Tans et al. 1990, Fan et al. 1998, Gurney et al. 2002), possibly attributed

to reforestation of abandoned agricultural lands and fire suppression (Hurt et al. 2002). Ecosystem modeling studies (Prentice and Lloyd 1998, Tian et al. 1998, 2000) and some empirical studies (Grace et al. 1995, Malhi et al. 1998, Phillips et al. 1998) have suggested that tropical forests might be large terrestrial sinks.

Undisturbed tropical forests have historically been presumed to contribute little to changes in atmospheric carbon dioxide. Large areas of undisturbed forest in Amazonia are typically uneven aged with many large trees, indicating the long periods of succession assumed suitable for attaining carbon equilibrium (Anderson and Spencer 1991). However, tropical forests account for 40% of carbon stored globally in terrestrial biomass (Dixon et al. 1994) and contribute as much as 36% of the net exchange between atmosphere and terrestrial vegetation (Melillo et al. 1993). Thus, small changes in net carbon balance of undisturbed tropical

Manuscript received 2 May 2002; revised 23 October 2002; accepted 6 November 2002. Corresponding Editor: W. L. Silver. For reprints of this Special Issue, see footnote 1, p. S1.

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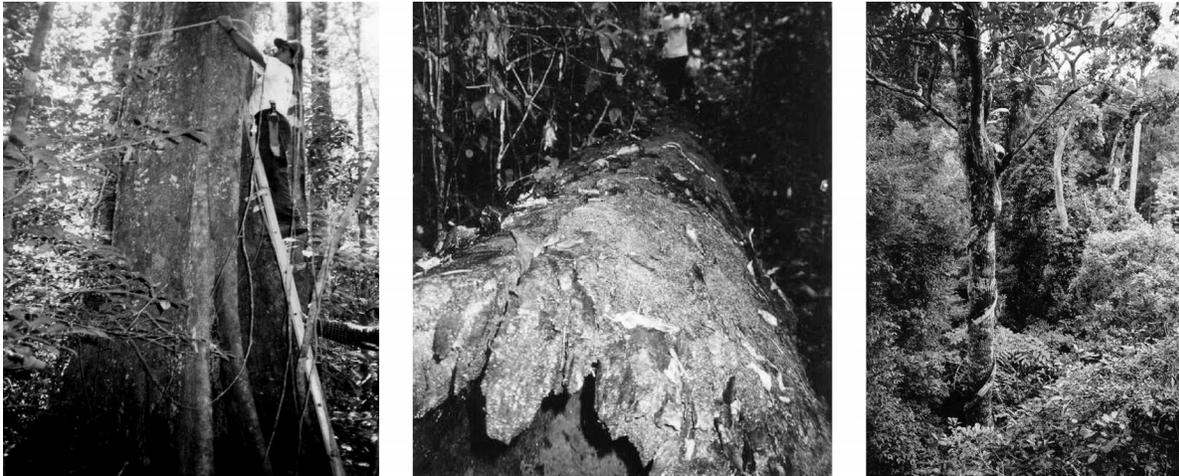


PLATE 1. (Left) Mateiro measuring a large buttressed tree with tape, (center) a large piece of coarse woody debris, and (right) a canopy tree within a gap. Photo credit: Lucy Hutyra.

forests could result in significant storage or release of carbon to the atmosphere. The high productivity of these forests may make them particularly responsive to growth enhancement from rising atmospheric carbon dioxide concentrations (Prentice and Lloyd 1998, Tian et al. 1998). Therefore, the role of tropical forests in the global carbon cycle remains a key scientific question.

Several recent studies have focused on potential carbon storage by primary tropical forests by examining their carbon flux and dynamics. Short-term (≈ 1 yr or less) eddy-covariance studies of carbon exchange reported significant accumulation of carbon in two tropical forests, with net uptake of $1.1\text{--}5.9$ Mg C \cdot ha $^{-1}\cdot$ yr $^{-1}$ carbon (Grace et al. 1995, Malhi et al. 1998). However, stand-level inhomogeneities and observational artifacts of the eddy-flux method make the interpretation of these observations problematic. In addition, interannual variations of stand-level carbon fluxes (Goulden et al. 1996, Tian et al. 1998, Barford et al. 2001) and of the global carbon budget (Marston et al. 1991, Keeling et al. 1996) indicate the need to characterize carbon balance over the long term in a variety of tropical forests.

Phillips et al. (1998) used inventories for widely distributed forest plots to infer average net storage of 0.71 ± 0.34 Mg C \cdot ha $^{-1}\cdot$ yr $^{-1}$ in live biomass of undisturbed tropical forests, with neotropical forests dominating uptake. The long time scale and extensive spatial coverage of these aggregated measurements should account for interannual and stand-level variations. However, these sites were not originally established to study carbon budgets, and may suffer from inadequate plot size (< 2 ha), bias in plot selection, uncertain site history, and measurement inconsistencies (Phillips and Gentry 1994, Clark and Clark 2000, Clark 2002); the significance of these potential methodological prob-

lems has generated some debate (Clark 2002, Phillips et al. 2002). An additional issue is the neglect of coarse woody debris (CWD). Stocks of CWD can be large (42% of aboveground live woody biomass in a Costa Rican forest [Clark et al. 2002]) and turnover times short (6–10 yr, Chambers et al. 2000, 2001a), thus changes in CWD can account for substantial carbon fluxes.

In this paper, we report on the first two-plus years of biometric data from a long-term study combining ground-based biometry with whole-system carbon dioxide fluxes (using eddy covariance) in an old-growth tropical forest designed to address the question of carbon balance and its ecological and climatic drivers in Amazon forests. We analyze data for aboveground woody growth increment, tree recruitment and mortality, CWD, and fine litterfall, to estimate aboveground net ecosystem production (NEP). The focus is on measurements of pool sizes and changes in pool sizes of live and dead wood, the carbon pools with relatively long turnover times. We focus on NEP, the difference in carbon inputs (NPP), and outputs (heterotrophic respiration), because the net change in stored ecosystem carbon is most appropriate for assessing terrestrial sources and sinks for atmospheric carbon dioxide.

METHODS

The site

The site is located in the Tapajós National Forest ($54^{\circ}58'$ W, $2^{\circ}51'$ S, Pará, Brazil), accessed by an entrance road at kilometer 67 along the Santarém–Cuiabá Highway (BR-163). As part of the Large-scale Biosphere–Atmosphere Experiment in Amazonia (LBA), an international research initiative led by Brazil, we have installed permanent forest research transects and an eddy-flux tower 1 km east of the access road (GPS

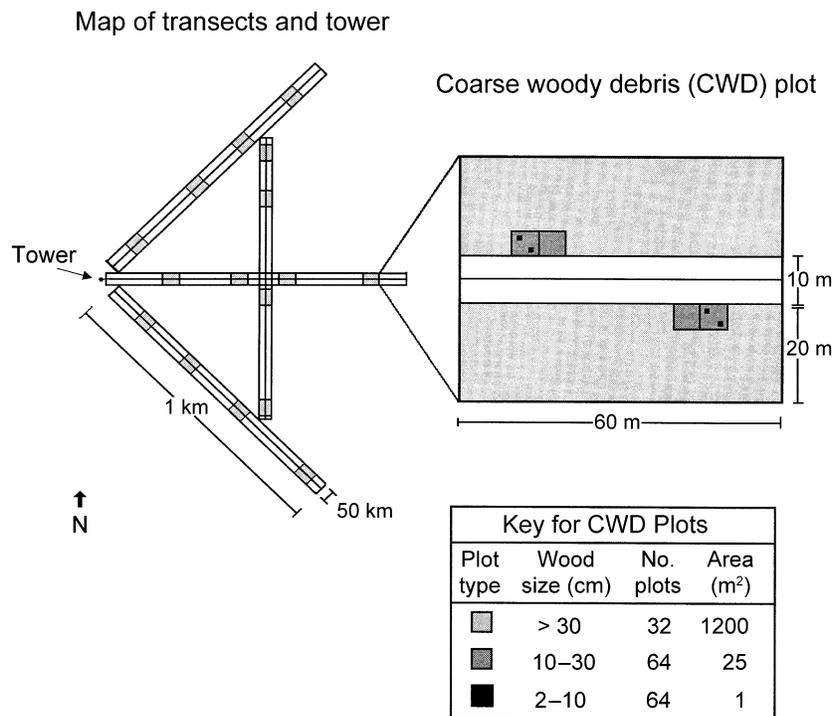


FIG. 1. Map of transects and CWD plots for kilometer 67 site in the Tapajós National Forest, Brazil.

coordinates: UTM zone 21M, 726889 E, 9684049 N). Temperature, humidity, and rainfall average 25°C, 85%, and 1920 mm per year, respectively (Parotta et al. 1995). Soils are predominantly nutrient-poor clay oxisols with some sandy utisols (Silver et al. 2000), both of which have low organic content and cation exchange capacity. The canopy has a significant number of large emergent trees (to 55 m height), *Manilkara huberi* (Ducke) Chev., *Hymenaea courbaril* L., *Bethollletia excelsa* Humb. and Bonpl., and *Tachigalia* spp., and a closed canopy at ~40 m. With large logs, many epiphytes, uneven age distribution, and emergent trees, the forest can be considered primary, or “old-growth” (Clark 1996). It shows no signs of recent anthropogenic disturbance other than hunting trails.

*Live biomass, growth, mortality,
and recruitment measurements*

Four permanent 50 × 1000 m transects were installed adjacent to the eddy-covariance tower in July of 1999 (Fig. 1), accounting for 19.75 ha of surveyed forest. Three transects originate near the tower and run in the predominant wind directions from the tower (northeast, east, and southeast), while the fourth runs north–south, intersecting the east transect at 550 m. The long, continuous transects aim to incorporate spatial heterogeneity throughout the tower footprint, avoiding bias associated with small scattered plots that can be disproportionately influenced by emergent trees. Trees ≥35 cm dbh (diameter at breast height) ($n = 949$) were

identified to species, tagged, measured, and mapped (Table 1). Trees ≥10 cm dbh ($n = 1646$) were identified to species, tagged, measured, and mapped in narrower transects (four each 10 × 1000 m, for a total area of 3.99 ha) running down the middle of the larger transects. Whole-sample measures reported on an areal basis (stems per hectare, growth rate per hectare, etc.) were calculated as a per-area weighted sum of small (10 cm < dbh < 35 cm) and large tree (≥35 cm dbh) samples. Trees with significant buttresses were measured above buttress termination (see Plate 1).

Stainless steel dendrometer bands were placed on a random subsample of 1000 trees, stratified by taxonomic family and size class, in December 1999 (Table 1). The 48 identified taxonomic families were divided into five size classes (10–<22.5, 22.5–<35, 35–<55, 55–<90, and ≥90 cm dbh). We included all individual trees in the largest size class (≥90 cm dbh), because large trees account for a major portion of aboveground biomass in neotropical forests (Brown et al. 1995, Clark and Clark 1996). The rest of the sample was drawn randomly from the remaining size-class–taxonomic-family categories, with a probability proportional to $1/\sqrt{d_i}$, where d_i was the stem frequency of trees in category i . This sampling strategy ensures that all size classes and the full diversity of life-history traits (as represented by taxonomic family) were sampled, but avoids repetitively sampling the large number of stems in smaller subgroups that have more limited influence on carbon balance. We banded a large number of trees

TABLE 1. Measurements of biomass pools and fluxes at kilometer 67, Tapajós National Forest, Brazil.

Pool or flux and measurement method	Size class	Area	<i>n</i>	Frequency
Live aboveground biomass				
dbh survey	>35 cm dbh	19.75 ha	~1000 stems	2 yr
dbh survey	10–35 cm dbh	3.99 ha	~1800 stems	2 yr
Growth increment				
dbh comparison	>35 cm dbh	19.75 ha	951 stems	2 yr
dbh comparison	10–35 cm dbh	3.99 ha	1610 stems	2 yr
dendrometers	>10 cm dbh	19.75 ha	1000 stems	6 wk
Mortality				
dbh survey	>35 cm dbh	19.75 ha	30 stems	2 yr
dbh survey	10–35 cm dbh	3.99 ha	57 stems	2 yr
Recruitment				
dbh survey	10–35 cm dbh	3.99 ha	201 stems	2 yr
Standing CWD				
stem survey	>10 cm dbh	19.75 ha	539 snags	once
Fallen CWD				
plot-based survey	>30 cm diam.	32 plots, each 120 m ²	246 pieces	once
plot-based survey	10–30 cm diam.	64 plots, each 25 m ²	191 pieces	once
plot-based survey	2–10 cm diam.	64 plots, each 1 m ²	390 pieces	once
line-intercept survey	>10 cm diam.	200 lines, each 10 m long	249 pieces	once
line-intercept survey	2–10 cm diam.	40 lines, each 1 m long	238 pieces	once
Litter fall				
litter traps	<2 cm diam.	40 × 0.43 m ²	...	2 wk

Note: CWD = coarse woody debris.

with the goal of obtaining high-resolution growth measurements that could be correlated to precipitation or seasonality with errors <10%.

An initial baseline dbh was measured and canopy status was assessed for banded trees in February 2000 (two months after band installation). Classes were assigned reflecting each tree's actual status relative to the nearby canopy. Trees whose crowns rose above the surrounding canopy were classified as "emergent," trees reaching the canopy were labeled "canopy," trees whose crown remained just below the canopy were labeled "subcanopy," and trees whose crown remained well below the canopy were labeled "suppressed." Dendrometer band increments, or expansion of the bands with tree growth, were subsequently measured every 4–6 wk using electronic calipers, allowing detailed examination of variation in seasonal growth rates.

The permanent transect plots were resurveyed in 2001 to give estimates of growth, mortality, and recruitment. The dbh of the 1000 subsampled trees with dendrometers was remeasured in April 2001, while the dbh of remaining nonbanded trees was remeasured in July 2001, providing a 2-yr growth increment for trees that survived the sampling interval. The April 2001 dbh survey of banded trees was adjusted to the full 2-yr interval by adding 3 mo (April through July) of growth as measured by the dendrometer bands. Trees with no foliage and dry sapwood all around the tree were recorded as dead. Previously untagged trees,

which had grown into the minimum size classes ($n = 201$ for 10-cm size class, $n = 94$ for 35-cm size class), were inventoried and trees growing into the smallest (10 cm) size class were added to the sample as recruitment.

Best-estimate whole-tree biomass was calculated from tree dbh measurements using an allometry (Chambers et al. 2001a) derived from trees in two forest sites north of Manaus, Amazonas, Brazil. We consider it to be a best estimate due to the relative similarities between forests in Manaus and the Tapajós. In order to make an estimate of allometric uncertainty for comparison, we also used two allometries (Eqs. 3.2.3 and 3.2.4) from Brown (1997), derived from worldwide tropical forest data.

Tree growth increments were calculated for the two different live tree measurement methods (Table 1). For the repeated dbh surveys of 1999 and 2001, growth arises from the subset of trees alive in both data sets and was calculated as the pairwise difference in biomass between 1999 and 2001 ($n = 2561$). Field measurement errors were corrected by removing trees with growth rates outside of the central 99% of the frequency distribution of growth rates (i.e., trees with growth rates <−4.8 cm/yr or >5.3 cm/yr, $n = 56$). This is an unbiased method to exclude outliers resulting from measurement errors such as misread dbh tapes. Sampling uncertainty on growth was also estimated using bootstrap analyses (1000 bootstrap samples of growth interval, the 95% confidence interval reported).

For the dendrometer survey, growth was determined as the addition of the increment measured by the dendrometer to the initial dbh for each tree. The 1000-tree dendrometry subsample was scaled up to per unit area flux (G , in $\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) by the following sum:

$$G = \frac{1}{\Delta t} \sum_{i=1}^{N_c} d_i \overline{\Delta B_i}$$

where Δt is the sampling interval, d_i is the observed stem density from the original inventory (number of trees per hectare), and $\overline{\Delta B_i}$ is the measured mean biomass increment in the dendrometry subsample (Mg C per tree), both in the i th size-class–taxonomic-family category, and N_c is the number of such stratification categories.

Losses from the pool of live biomass through mortality were accounted in the 2001 resurvey of all stems. The biomass for each tree that died was determined using the same allometric equations applied to live biomass and employing last measured dbh prior to death.

Biomass additions due to recruitment (individuals growing into the 10-cm size class) were determined with the same allometries. Previously untagged trees whose sizes were greater than $10 \text{ cm} + g_{99}$, where g_{99} is the 99th percentile of the 2-yr species-specific growth distribution, were deemed to have been mistakenly missed in the original survey, and thus not true recruitment. These individuals were added into the 1999 data set and the growth data set, with their dbh in 1999 back calculated from 2001 measurements, using the species' average annual growth rates.

Coarse woody debris (CWD) measurements

All standing dead stems ≥ 10 cm dbh in the entire 19.75 ha and taller than 1.3 m were measured, tagged, identified to common name, and assigned to a decay class in April 2001. Measurements of dbh of standing dead trees were used to find an estimate of top diameter using Chambers et al.'s (2000) taper function and then were converted to volumes using the formula for a frustum of a cone (Harmon and Sexton 1996). In July 2001, we made dimensional measurements of fallen CWD (see Plate 1) in a series of nested plots within the 19.75 ha used for live biomass measurements (Table 1, Fig. 1). All fallen debris >30 cm in diameter and 1 m in length were tagged, measured, and assigned to decay classes in 32 20×60 m plots randomly placed in pairs along the biomass transect lines. All debris from 10 to 30 cm in diameter were measured in 64 5×5 m subplots, and all debris from 2 to 10 cm were measured in 64 1×1 m subplots, randomly located within the 5×5 m plots (Fig. 1). Decay classes used for both standing and fallen CWD were: decay class 1, solid wood, recently fallen, bark and twigs present; decay class 2, solid wood, significant weathering, branches present; decay class 3, wood not solid, may be sloughing but nail still must be pounded into tree;

decay class 4, wood sloughing and/or friable, nails may be forcibly pushed into log; and decay class 5, wood friable, barely holding shape, nails may be easily pushed into log. Dimensional measurements were converted to volumes, using Newton's formula for a cylinder (Harmon and Sexton 1996).

Biomass estimates for CWD were calculated by combining measured volumes with measured decay-class specific CWD densities obtained from a CWD density study conducted at a nearby site, also in the Tapajós National Forest (at kilometer 83, 17 km south of the site described here). For CWD >10 cm diameter, logs ($n = 258$) were selected for sampling based on a random, size-class stratification. Logs were initially sawed in two places yielding cylinders 5–8 cm in height. Cylinders were digitally photographed and then the photograph was analyzed for wood and void sections to calculate percent void space for each cylinder. Each cylinder was sampled by extracting wood plugs ($n = 634$ for the 258 logs) with a tenon cutter attached to a portable power drill. Plugs were extracted every 5 cm from the center of the cylinder along one of eight evenly spaced radii selected at random. Fresh plug volumes were estimated using a cylinder calculation. Plugs were then labeled and dried for three months at 65°C and weighed. Density was calculated by dividing dry mass by fresh volume for each plug and then averaging for each tree sampled with a multiplicative adjustment for the total wood volume ($1 - \text{fraction of void space}$). Uncertainty on density was estimated from the variation across samples within each decay class. Final density estimates for each decay class were determined by averaging adjusted densities for trees sampled within a decay class and weighting them according to the inverse of sampling frequency. For more details, see Keller et al. (*in press*).

For comparison, necromass was also estimated using wood density numbers from other tropical forests in Delaney et al. (1998), Summers (1998), and Clark et al. (2002). We represent sampling uncertainty for CWD biomass with 95% confidence intervals calculated using a bootstrap analysis with 1000 bootstrap simulations using individual CWD pieces as the unit of replication. The biomass errors for CWD represent the combination of volume sampling uncertainty and density uncertainty.

For comparison, additional measurements of CWD pools were made at the kilometer 67 site using the line-intercept method (Van Wagner 1968, Brown 1974; Table 1). In January 2002, 2000 m of line was run, in 10-m segments, measuring pieces greater than 10 cm in diameter and 400 m of line, in 10-m segments, measuring pieces >2 cm in diameter. The line-intercept survey estimates of CWD volumes ($\sim 164 \text{ m}^3/\text{ha}$) agreed with the plot based estimates ($\sim 152 \text{ m}^3/\text{ha}$), within sampling uncertainty (1000 bootstrap simulations, using each individual CWD line segment as the

TABLE 2. Aboveground biomass pool sizes (Mg C/ha) and fluxes (Mg C·ha⁻¹·yr⁻¹) between July 1999 and July 2001 (all uncertainties are 95% CI).

Pool or flux (<i>n</i> = no. stems)	Best estimate†	Alternate A‡	Alternate B§
A) Live biomass			
Pool size in trees >10 cm dbh			
1999 (<i>n</i> = 2648)	143.7 (± 5.4)	154.4 (± 9.0)	161.4 (± 11.1)
2001 (<i>n</i> = 2803)	147.4 (± 5.9)	157.9 (± 8.8)	164.5 (± 12.0)
Fluxes to aboveground live biomass in trees >10 cm dbh			
Recruitment (<i>n</i> = 180)	0.63 (± 0.09)	0.53 (± 0.08)	0.53 (± 0.08)
Growth (<i>n</i> = 2561)	3.18 (± 0.20)	3.25 (± 0.22)	3.11 (± 0.28)
Mortality (<i>n</i> = 87)	-2.41 (± 0.53)	-2.51 (± 0.65)	-2.55 (± 0.75)
Net flux	1.40 (± 0.62)	1.27 (± 0.80)	1.09 (± 0.92)
B) Coarse woody debris (CWD)			
Pool size in standing trees (>10 cm dbh) and fallen (>2 cm) pieces	48.0 (± 5.2)	NA	NA
Fluxes to CWD			
Mortality	2.4 (± 0.5)	2.5 (± 0.7)	2.6 (± 0.8)
Respiration	-5.7 (± 1.0)	-4.0 (± 0.4)	-8.2 (± 0.9)
Net flux	-3.3 (± 1.1)	(range -1.4 to -5.8)	
C) Total aboveground biomass (live biomass + CWD)			
Pool size	195.4 (± 7.9)	205.9 (± 9.8)	212.5 (± 13.1)
Net flux	-1.9 (± 1.0)	(range -0.1 to -4.5)	

† Values are derived using the Chambers et al. (2001a) Amazon allometry for tree biomass and the decay-class-specific respiration rates for CWD respiration, adjusted for slower decomposition of standing dead wood (see Table 4). Allometry is: $\ln[\text{tree mass}] = -1.06 + 0.333 \ln(\text{dbh}) + 0.933 \ln(\text{dbh})^2 - 0.122 \ln(\text{dbh})^3$, with dbh in centimeters and tree mass in kilograms C in biomass (assuming 1 kg dry biomass = 0.5 kg C biomass).

‡ Values are derived using Brown's (1997) universal tropical allometry (Eq. 3.2.3 in Brown [1997]) for tree biomass, and a lower-bound CWD respiration rate constant of $k = 0.0825 \text{ yr}^{-1}$, the average of respiration rates across non-pine forests in the southern United States (Turner et al. 1995). Allometry is: $\text{Tree mass} = 21.345 - 6.4 (\text{dbh}) + 0.621 (\text{dbh})^2$.

§ Values are derived using Brown's (1997) universal tropical allometry (Eq. 3.2.4 in Brown [1997]) for tree biomass, and an upper-bound respiration rate constant of $k = 0.17 \text{ yr}^{-1}$ for CWD respiration. Allometry is: $\ln[\text{tree mass}] = -2.827 + 2.53 \ln(\text{dbh})$.

|| Flux ranges give a highly conservative uncertainty analysis, based on the largest and smallest possible sums of inflow and outflow permutations (within consistent allometries) in the "best estimate," "alternate A," and "alternate B" columns.

TABLE 3. Coarse woody debris densities, respiration rates, pool sizes, and respiration, by decay class.

Decay class	Density (Mg biomass/m ³)	<i>k</i> † (yr ⁻¹)	Volume (m ³ /ha)		Mass (Mg C/ha)	Respiration (Mg C·ha ⁻¹ ·yr ⁻¹)
			Fallen	Standing		
1	0.60 (± 0.04)	0.091	20.6	1.1	6.5 (± 2.5)	0.6
2	0.70 (± 0.06)	0.063	26.2	6.4	11.4 (± 3.2)	0.7
3	0.58 (± 0.06)	0.099	35.2	13.0	14.0 (± 3.8)	1.4
4	0.45 (± 0.06)	0.162	45.2	7.5	11.9 (± 2.6)	1.9
5	0.28 (± 0.06)	0.314	24.5	6.3	4.3 (± 1.4)	1.4
Total			151.7 (± 19.4)	34.3 (± 7.6)	48.0 (± 5.2)	6.0 (± 0.7)
Total CWD respiration adjusted for slower decomposition of standing dead wood:‡						5.7 (± 1.0)

Note: Error measurements are 95% CI.

† Decay-class-specific CWD respiration rate derived from $k = \exp(b\rho)$, where $b = -4.117 \pm 0.62$ (mean ± 1 SE), ρ = density (Chambers et al. 2001b), and an unbiased estimate of mean k assuming normal distribution of the exponent is $\bar{k} = \exp(-4.117\rho + 0.5[0.62\rho]^2)$ (Gut 1995).

‡ Standing dead wood is observed to have a substantially lower respiration rate (Chambers et al. 2001b); accordingly, adjusted respiration is lower because it assumes all standing CWD respire at the moderately low rate of decay class 1, and its confidence interval is wider than the purely statistical interval by an amount equal to the downward adjustment (0.3 Mg C·ha⁻¹·yr⁻¹).

TABLE 4. Coarse woody debris pools segregated by size class and standing/fallen status, in terms of directly measured volume and calculated mass.

CWD size class (cm)	No. pieces	Volume (m ³ /ha) [†]			Mass (Mg C/ha)
		Fallen CWD	Standing CWD	Total CWD	
>30	456	97.7 (± 14.7)	31.6 (± 6.3)	129.4 (± 17.6)	33.9 (± 5.2)
10–30	520	34.6 (± 5.8)	2.6 (± 0.2)	37.3 (± 7.3)	9.4 (± 1.5)
2–10	390	19.3 (± 6.4)	NA	19.3 (± 5.9)	4.7 (± 1.2)
Total		151.7 (± 19.4)	34.3 (± 7.6)	186.0 (± 18.4)	48.0 (± 5.2)

Note: Values are mean and 95% CI.

[†] Volume of fallen CWD + volume of standing CWD = total CWD volume.

unit of replication). However, sampling uncertainty around the line-based estimates was larger (>20% of the mean), despite the relatively long line lengths. Because of this higher uncertainty in the line-intercept survey, we report values and analysis using the plot-based measurements (Tables 2B, 3, and 4).

To examine change in the stock of the CWD pool, we compared measured mortality inputs (using the methods described above) to CWD respiration losses. We estimated these losses by assuming respiration follows first-order kinetics, $\text{respiration} = k \times (\text{total CWD biomass})$, where the plausible range for CWD respiration was bracketed by using three different approaches. The first (best-estimate) approach uses a separate k for each decay class, calculated from the expression

$$k = 10^{(-1.788 \pm 0.27(\text{SE}))\rho} = \exp([-4.117 \pm 0.62(\text{SE})] \times \rho)$$

derived from CWD respiration studies in tropical forest near Manaus, Brazil (Chambers et al. 2001b), and from our decay-class specific densities, ρ (Tables 4 and 5). Since k is lognormal, we calculated the decay-class-specific rates from the expression for the mean of a lognormal distribution, which is affected by its variance: $\bar{k} = \exp(-4.117\rho + [0.5][0.62\rho]^2)$ (Gut 1995). The second and third approaches use upper and lower bound k 's, respectively, which were applied to whole-forest CWD mass, regardless of decay class. Upper-bound $k = 0.17 \text{ yr}^{-1}$, from a study of CWD mass loss over 10–15 yr in a tropical forest near Manaus (Chambers et al. 2000). Lower bound $k = 0.0825 \text{ yr}^{-1}$, based on an average across non-pine temperate forests (oak–hickory, and bottomland hardwoods) in the southern United States (Turner et al. 1995). Both of these values are for average annual whole-forest conditions and for CWD from a range of decay classes.

The upper bound k is probably too high, because it includes the lost mass of fragmented material that is not immediately respired to the atmosphere. The lower bound k is almost certainly too low for this tropical forest, since it is derived from midlatitude temperate forests. In our analysis, we use these two extreme values to bracket the conservative range of possible CWD respiration losses, and we used the first approach (along with the results of uncertainty analysis) to give a more plausible central best estimate.

Fine litterfall measurements

Litter collection began in July 2000 using 40 circular, mesh screen traps (0.43 m diameter, 0.15 m²) randomly located throughout the 19.75-ha tree-survey area. Every 2 wk, litter was collected, sorted, oven dried at 60°C, and weighed. The litterfall from each trap was sorted into (1) leaves, (2) fruits and flowers, (3) wood <2 cm diameter, and (4) miscellaneous. We report here on the 19-mo period from July 2000 through February 2002.

Uncertainty analysis

We quantified two kinds of uncertainties in general: sampling uncertainty and uncertainties due to nonstatistical sources of error (such as allometric uncertainty and possible biases due to applying parameters that were derived in other tropical forests, such as CWD respiration rates). Sampling uncertainties were quantified using bootstrap analyses (Efron and Tibshirani 1997), and nonstatistical uncertainties were quantified by bracketing a best estimate with possible alternate estimates intended to represent a maximum possible range of outcomes.

For bootstrap analyses, we used 1000 bootstrap samples. Stems were used as the unit of replication for carbon stocks and growth and mortality fluxes, and plot segments 50 m long were used as the unit of replication for recruitment. Unless otherwise indicated, 95% confidence intervals are reported as central estimate (plus or minus uncertainty). For brevity and a more conservative analysis, asymmetrical confidence limits (as with distributions that are lognormal) are reported symmetrically, where reported uncertainty is the maximum of (97.5 percentile – median) and (median – 2.5 percentile).

Because CWD respiration was based in part on application of respiration rates derived from studies at other sites (rather than measured directly here), we used an approach that was more conservative than a purely statistical one by combining the bootstrap sampling uncertainty with analysis accounting for potential sources of bias. First, for sampling uncertainty, the respiration of each piece of wood in each bootstrap sample was calculated from $\text{Respiration} = k \times (\text{CWD mass})$

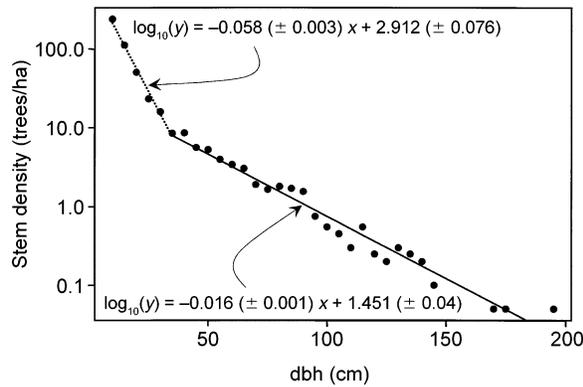


FIG. 2. Stem density (log scale) vs. dbh for the 2001 live biomass survey. Two different loglinear trend lines were fit to data for trees >40 cm dbh and <40 cm dbh (estimated regression coefficients ± 1 SE are shown).

= $\exp(b \times \rho) \times ([\text{CWD volume}] \times \rho)$, where CWD volume was the volume of the sample piece, b was drawn from its normal distribution (mean = -4.117 , 1 SD = 0.62 ; Chambers et al. 2001b), and ρ is drawn from a normal distribution with mean and standard deviations appropriate to the decay class of the sample piece. This gave an uncertainty estimate on CWD respiration that accounts for combined uncertainty in volume, density, and first-order rate constant, and accounts for the correlation between CWD mass and rate constant k (which arises because both depend on CWD density ρ).

In addition, we adjusted estimated respiration downward to account for the lower respiration rate of standing (vs. fallen) dead wood, a consequence of its lower moisture at a given density (Chambers et al. 2001b). The difference in respiration rate between standing snags and fallen dead wood is a bias that is not well quantified ($n =$ two standing dead snags in Chambers et al. 2001b), so we used a simple approach that assumed all standing CWD respire at the moderately low rate of decay class one (instead of at the rate associated with its actual decay class). To account for residual unknown bias, we expanded the 95% confidence interval (calculated via the bootstrap described above) by an amount equal to the downward adjustment. We used this downward-adjusted value, along with its associated expanded confidence interval, as our best estimate of whole-forest CWD respiration.

RESULTS

Live biomass pool and flux

We surveyed 2596 trees in 1999 and 2803 trees in 2001; stem density was 469 and 498 trees per hectare, respectively. The total aboveground live biomass (mean and 95% CI) was 143.7 ± 5.4 Mg C/ha in 1999 and 147.4 ± 5.9 Mg C/ha in 2001 (Table 2A, allometry from Chambers et al. 2001a). These values fall within

the range of previously published biomass estimates for similar primary neotropical forests (Brown and Lugo 1992, 1995, Gerwing and Farias 2000, Chave et al. 2001, Keller et al. 2001). However, live biomass for trees ≥ 35 dbh (99.4 Mg C/ha) was 12% greater than a nearby Tapajós survey reporting 88.5 Mg C/ha of biomass (Keller et al. 2001). Allometric uncertainty for standing biomass was about the same as sampling uncertainty, each less than $\pm 10\%$ (Table 2A). Larger trees (≥ 35 cm dbh) accounted for the main portion of total biomass (67%), though smaller trees (≥ 10 cm and <35 cm dbh) were much more common (1780 trees, 64% of stems).

The distribution of stem density vs. size was piecewise loglinear with a distinctly steeper slope for trees <40 cm dbh (Fig. 2). The size class at which the slope change occurs is about the same as the cutoff in our nested plot design (35 cm), but this shift in the density curve is not an artifact of the larger plot areas for trees ≥ 35 cm: the stem density distribution using only the smaller subtransects (on which all trees ≥ 10 cm were inventoried) was indistinguishable from Fig. 2. The steeper slope for small trees could represent non-steady-state forest demography (in-growth of released trees) or suppression of growth rates in the smaller size classes (excess in stem density for suppressed stems in smaller size classes). The latter would contradict the constant-slope loglinear relationship often assumed between dbh and tree density in demographic models (e.g., Gillespie et al. 1992, Keller et al. 2001).

The annual stand biomass growth increment was 3.18 ± 0.20 Mg C \cdot ha $^{-1}\cdot$ yr $^{-1}$ ($n = 2561$ trees, Table 2A) based on 1999 and 2001 dbh measurements, a mean diameter increase of 0.36 cm/yr. The diameter growth increment per tree increased with size until 40 cm dbh (Fig. 3), with no clearly discernable pattern for larger trees (error bars increase as samples sizes decrease in the larger size classes). In contrast, the mean biomass increment per-tree increases significantly with diameter (Fig. 3) due to the power-law relation in the allometry. Remarkably, the bulk of the stand biomass growth increment was in small trees (2.10 ± 0.17 Mg C \cdot ha $^{-1}\cdot$ yr $^{-1}$ for trees <35 cm dbh; Fig. 4a) because of the great numbers of individuals in the smallest size class. Biomass growth increment based on dendrometer measurements (1000 trees) were similar, 2.3 – 3.1 Mg C \cdot ha $^{-1}\cdot$ yr $^{-1}$ (range based on both allometric and sampling uncertainties). Growth rates were examined by taxonomic family, however, placement in the canopy (light availability) was a more significant factor (Fig. 5a).

Trees were recruited at a rate of 23 trees \cdot ha $^{-1}\cdot$ yr $^{-1}$, adding 180 new stems and 0.63 ± 0.09 Mg C \cdot ha $^{-1}\cdot$ yr $^{-1}$ to our pool of aboveground live biomass (Table 2A, Fig. 6). Stem recruitment rates ($4.8 \pm 0.9\%$) were elevated compared to rates for other undisturbed forests in the central Amazon, which average 1.84% (Laurance

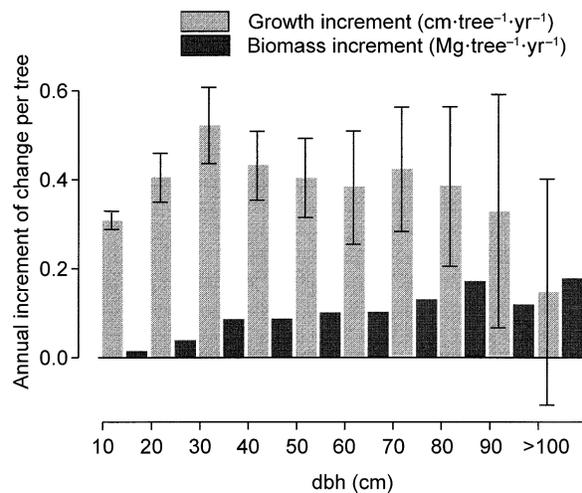


FIG. 3. Average annual growth increment per tree (cm·tree⁻¹·yr⁻¹, and 95% CI) and annual biomass increment per tree (Mg biomass·tree⁻¹·yr⁻¹), by dbh size class (the biomass increment was calculated using Chambers et al. [2001a] allometry). Growth increment per tree increases with size up to 40 cm dbh; above 40 cm dbh there is no discernible pattern because of large error bars due to small samples sizes.

et al. 1998, corrected to 2-yr sampling interval) with a range of 0.81 to 2.32% (Phillips and Gentry 1994). In order to evaluate the possibility that high recruitment is an artifact of missing trees in the original survey and counted in the resurvey, we examined the rate of trees crossing all size thresholds (ratio of trees crossing to trees in size class) to determine if the recruitment into the 10-cm size class was anomalously high. We observed that the rate of trees crossing into the 10–15 cm size class was not detectably different from the rate of trees crossing into other 5-cm size-class intervals (Table 5), and concluded that the high recruitment rates were not an artifact of trees overlooked in 1999.

Mortality (-2.41 ± 0.53 Mg C·ha⁻¹·yr⁻¹; Table 2A, Figs. 4a and 6) offsets accumulation of aboveground live biomass through growth and recruitment. Eighty-eight trees died in the 2-yr interval, giving an annualized stem mortality rate of 1.7%. This rate is slightly higher than both the average mortality rate measured at several other sites across the Amazon basin (1.5%), and the average measured at tropical sites across world (1.6%), but well within the 10th and 90th percentiles for both (Lugo and Scatena 1996). More small individuals (dbh < 35 cm) died (57 stems, ~66% of stems that died), but mortality in large trees (≥ 35 cm) accounted for a larger portion of the biomass lost (-1.59 ± 0.31 Mg C·ha⁻¹·yr⁻¹, ~66% of mortality losses) (Fig. 4a and b). The contrast with carbon gain in live biomass (dominated by smaller trees) is discussed next.

Dividing the live biomass pool by input (growth + recruitment) or outflow (mortality) gave turnover times of 38 and 59 yr, respectively, whereas the stem turnover

times, based on $4.8 \pm 0.9\%$ recruitment and 1.7% mortality, were 21 and 59 yr (geometric mean 31 yr). The stem turnover times are shorter than for other Amazonian forests: average turnover from mortality was 67 yr for 12 Amazonian sites (Lugo and Scatena 1996) and 80 yr (geometric mean of mortality and recruitment turnover times) for five other Amazonian sites (Phillips and Gentry 1994). Our site in the Tapajós is more dynamic than other Amazonian forests, this is possibly a response to a recent disturbance.

Growth, recruitment, and mortality combine to yield a net flux (uptake of carbon) in live biomass of 1.40 ± 0.62 Mg C·ha⁻¹·yr⁻¹ (Table 2A). This value is similar (Fig. 6) to the net flux measured in an aggrading temperate forest in central Massachusetts (Harvard Forest [Barford et al. 2001]; see Fig. 6), despite the much larger gross fluxes in Tapajós.

Fig. 4 summarizes the increase of biomass and stem density, which was notably concentrated in smaller trees where growth and recruitment exceed mortality and outgrowth. In the larger (60–85 cm) trees, mortality outstrips growth and recruitment (Fig. 4a). Stem density increased from 448 to 478 trees/ha (1.44 Mg C·ha⁻¹·yr⁻¹ biomass accumulation) in classes <60 cm, but was essentially stable (from 20 to 19 trees/ha, 0.04 Mg C·ha⁻¹·yr⁻¹ biomass loss) in classes ≥ 60 cm (Fig. 4).

Coarse woody debris: pool sizes and fluxes

CWD totaled 48.0 ± 5.2 Mg C/ha with a large fraction (18%, or 27 stems/ha) as standing dead snags (Table 4). CWD estimates using wood densities derived in other neotropical forests gave slightly lower numbers: 40.4 ± 5.2 Mg C/ha, 42.8 ± 4.5 Mg C/ha, and 31.9 ± 3.6 Mg C/ha (Delaney et al. 1998, Summers 1998, Clark et al. 2002, respectively). CWD exhibited high spatial variability (e.g., sixfold differences in average volume across the 16 large CWD plots in Fig. 1) but there was no detectable difference from a random pattern across the four transects.

The CWD pool is in the upper range of estimates from other tropical forests, though detailed comparisons are difficult due to incompatible measurement methods and size class delineations. Standing CWD falls in the range of other reported values (Clark et al. 2002, Delaney et al. 1998). The fallen CWD is higher: our estimate of fallen CWD (39.1 ± 5.7 Mg C/ha for pieces ≥ 2 cm, 34.4 ± 5.6 for pieces ≥ 10 cm) is roughly twice as much as found by Delaney et al. (1998) (16.6 Mg C/ha for fallen pieces ≥ 2 cm), Clark et al. (2002) (23 Mg C/ha for pieces ≥ 10 cm), and Brown et al. (1995) (15 Mg C/ha for pieces ≥ 10 cm). Total CWD ≥ 10 cm (44.0 Mg C/ha) was significantly higher than Summers (1998) estimate of 32.3 Mg C/ha for a nearby forest in Manaus. There is also evidence that the CWD at kilometer 67 is larger than other areas of the Tapajós. Volume estimates for fallen CWD at our site by the plot method (151.7 ± 19.4 m³/ha) and the line-intercept method (164.2 ± 38.1 m³/ha) are both ~50% higher

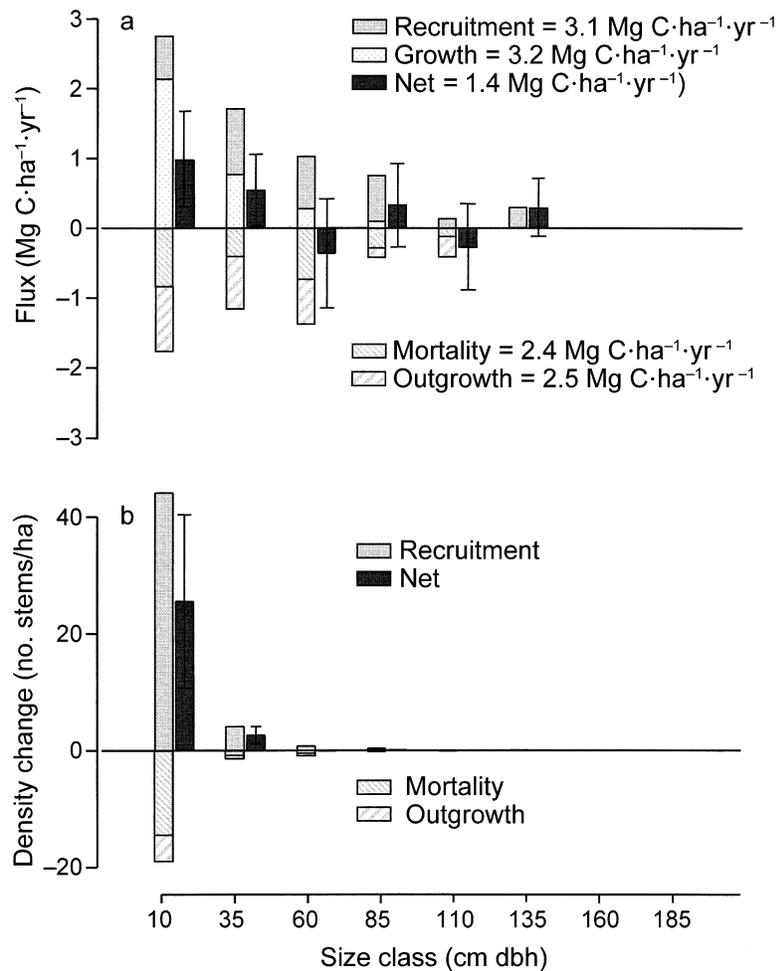


FIG. 4. (a) Gross fluxes to aboveground live biomass (allometry from Chambers et al. [2001a]) by size class due to growth, mortality, and recruitment (light gray, stippled, and hatched bars), and corresponding net flux (and 95% CI; dark gray bars) showing carbon accretion in small size classes and carbon loss from larger size classes. Recruitment for the smallest size class was due to "grow-ins" or previously unsurveyed stems; in subsequent classes, trees that grew across size-class limits were added into the new size class ("ingrowth") and subtracted from the preceding class as "outgrowth" (wide-hatched bars). (b) Gross changes in tree stem density (trees/ha) by size class due to ingrowth, mortality, and outgrowth (light gray and narrow-hatched bars), and corresponding net changes in stem density (dark gray bars).

than in the nearby forest at kilometer 83 (109 m³/ha by line intercept, data not shown). Note that our forest at kilometer 67 also had greater biomass in the largest trees (99.4 vs. 88.5 for trees ≥ 35 cm).

Mortality inputs to the pool of CWD from dying trees (Table 2B) were outstripped by respiration losses. The best estimate of CWD respiration, after adjusting for the slower respiration of standing dead wood, was 5.7 ± 1.0 Mg C·ha⁻¹·yr⁻¹ (Table 3), indicating an effective whole-forest CWD respiration rate of $k = 0.119$. The net result was loss from the CWD pool of 3.3 ± 1.1 Mg C·ha⁻¹·yr⁻¹ (1.4–5.8 Mg C·ha⁻¹·yr⁻¹ for the most conservative range) (Table 2B).

Aboveground biomass and flux in total: live and dead

Combining data for live and dead pools gives total aboveground biomass of 195.4 ± 7.9 Mg C·ha⁻¹·yr⁻¹ (trees with dbh ≥ 10 cm and CWD ≥ 2 cm, Table 2C), with ~76% alive and 24% dead. The best-estimate net flux to aboveground biomass was -1.9 ± 1.0 (negative carbon storage, Table 2C) at this site over the 2-yr period of the study, despite the large uptake by growing trees. The most conservative range of net flux was -0.1 to -4.5 Mg C·ha⁻¹·yr⁻¹; carbon storage in aboveground biomass is excluded with very high probability.

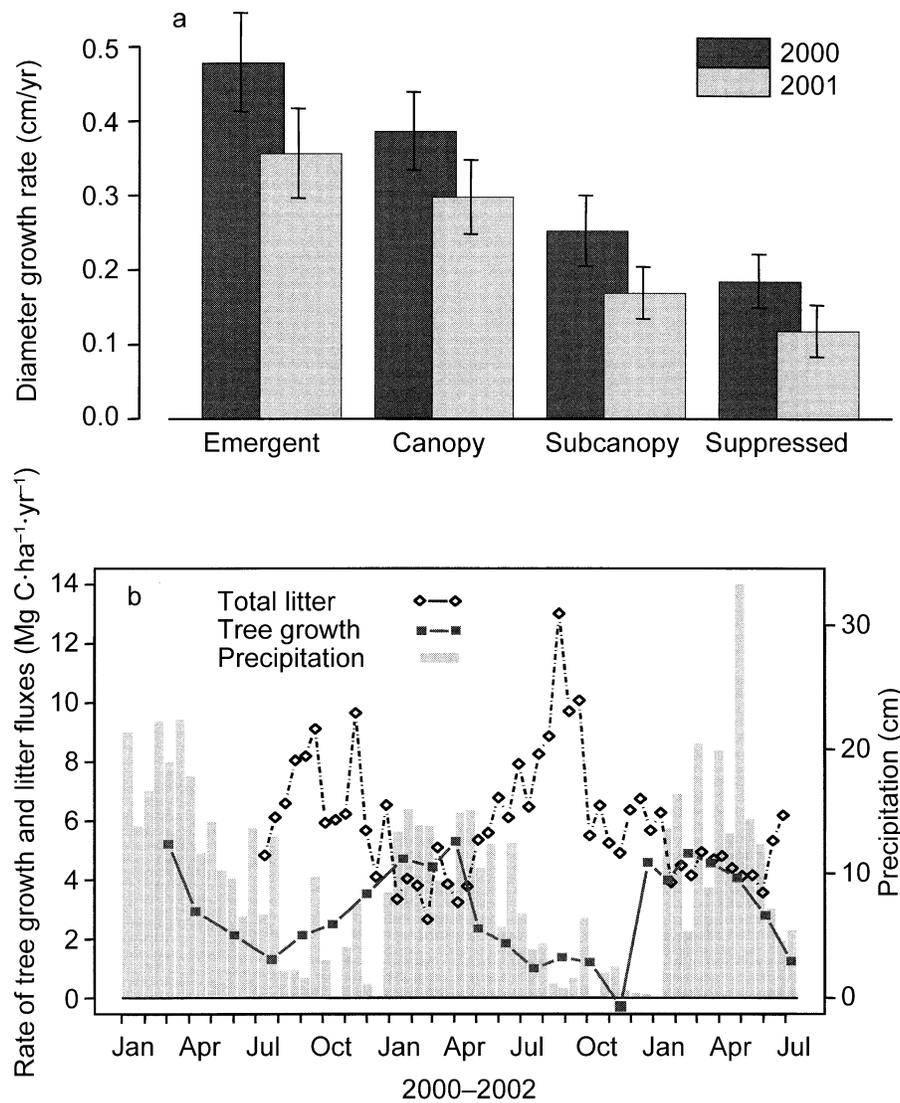


FIG. 5. (a) Mean tree growth increment (and 95% CI), by canopy status and year (dendrometry sample, February 2000–February 2002). Growth rate increases with light availability (as indicated by canopy status) and water availability (as indicated by annual precipitation: 2200 mm in 2000, 1846 mm in 2001 [Nepstad et al. 2002]). Mean dbh in 2001: emergent, 73.7; canopy, 35.2; subcanopy, 19.8; suppressed, 15.9. (b) Growth fluxes to aboveground tree biomass (February 2000 through July 2002) and in litterfall (July 2000 through July 2002), together with biweekly precipitation (Nepstad et al. 2002). Flux–precipitation correlations are: tree growth, $r = +0.71$, $P < 0.001$; litterfall, $r = -0.4$, $P < 0.005$. Biomass increments were calculated using Chambers et al. (2001a) allometry.

Fine litter: pool size and flux

Litterfall was $5.73 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in the first year and $6.32 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in the second year for all litter, including fruits, flowers, and wood < 2 cm diameter. Leaves accounted for $\sim 70\%$ both years. Total litter was somewhat higher than the range reported by most other studies of moist tropical forests ($3.65\text{--}4.15 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$; Klinge and Rodrigues 1968, Franken 1979, Luizao and Schubart 1987, Luizao 1995), lying at the upper end of the range ($0.9\text{--}6.0 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) given

by Clark et al. (2001) for the tropics as a whole. The high litterfall rate suggests that this site may have an unusually high leaf area, and/or more rapid leaf turnover, than other neotropical forests.

Fine litter fluxes exceed the growth flux to aboveground live wood and contribute significantly to NPP. Because litter turnover time is short, on the order of one year (Klinge and Rodrigues 1968, Brown and Lugo 1982), litter fluxes are balanced by decomposition on the time scale of several years. Thus we did not include litter in our net carbon storage calculations.

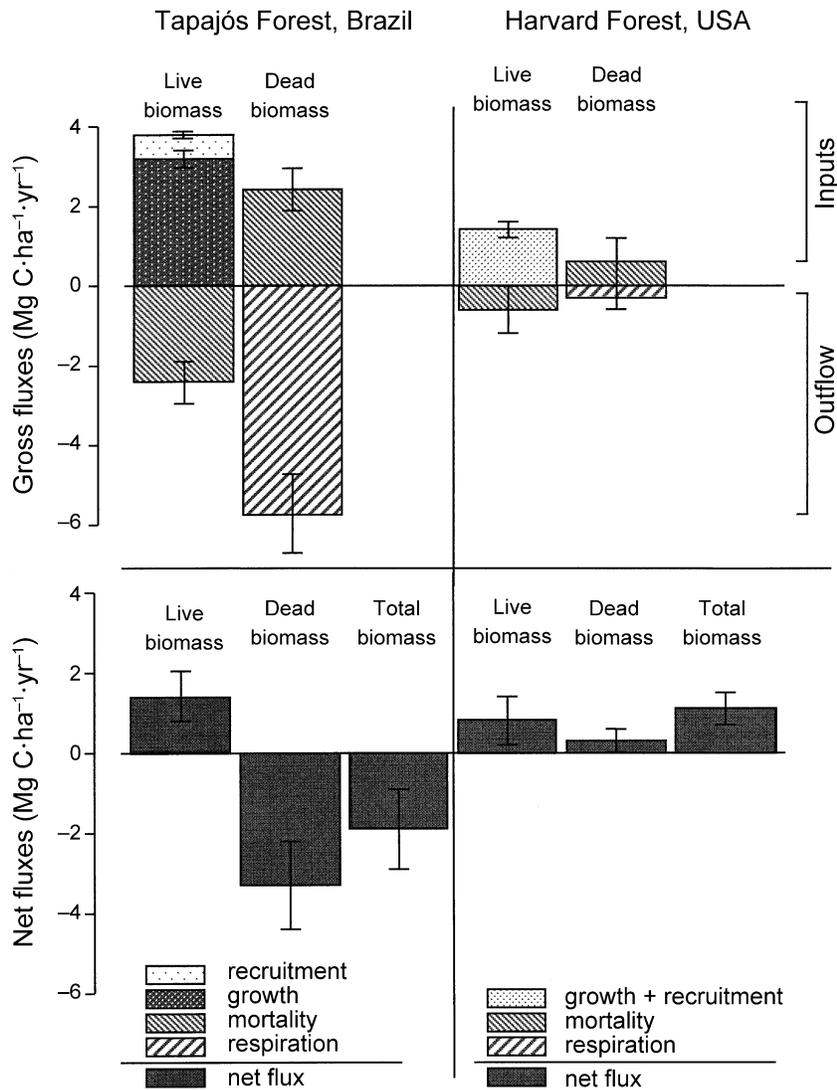


FIG. 6. Gross and net fluxes to live, dead, and total aboveground biomass (mean and 95% CI) in the Tapajós National Forest and in a temperate mid-latitude forest (Harvard Forest, Petersham, Massachusetts, USA). Live biomass uptake in the Tapajós Forest is indistinguishable from that at Harvard Forest; however, the temperate forest has carbon gains for the dead biomass and the total aboveground biomass pools while the Tapajós has large net losses.

Ecological and climatic controls on tree growth and fine litterfall

Canopy status (correlated with light availability) and year (a surrogate for annual precipitation input) together account for statistically significant variance in annual stem diameter growth increments in the dendrometry sample (two-way ANOVA, with both factors highly significant: canopy status $F_{3,1933} = 43.7$, $P < 0.0001$; year $F_{1,1933} = 25.5$, $P < 0.0001$). Suppressed and subcanopy trees grew at significantly smaller rates than canopy and emergent trees, and growth in the wet year (February 2000 to February 2001, precipitation = 2412 mm) significantly exceeded the dry year (February 2001 to February 2002, precipitation = 1805

mm) growth (Fig. 5a). Precipitation also correlated with tree growth at the monthly time scale (Pearson correlation coefficient, $r = 0.71$, $P < 0.001$; Fig. 5b). Litterfall also correlated with rainfall, but in the opposite sense (biweekly litterfall vs. precipitation correlation, $r = -0.4$, $P < 0.01$) (Fig. 5b).

DISCUSSION

Aboveground biomass measurements for the two-year study period indicate net emission of carbon from this site ($1.9 \pm 1.0 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ [mean and 95% CI]), an apparent contrast with both the eddy-covariance studies that report net carbon uptake in similar Amazonian forests (Grace et al. 1995, Malhi et al. 1998),

TABLE 5. The number of stems crossing a size class threshold (every 5 cm) vs. the number of stems originally in a size class, expressed as raw numbers and as an annualized percentage rate.

Threshold (cm)†	No. stems crossing threshold	No. stems originally present in size class	Rate of stems crossing threshold (%·yr ⁻¹)
10	201‡	882	11
15	78	419	9
20	36	192	9
25	21	92	11
30	19	61	16
35	11	32	17
40	33	167	10
45	35	99	18
50	18	101	9
55	17	75	11
60	15	71	11
65	19	52	18
70	6	54	6
75	12	40	15
80	11	24	23
85	5	43	6
90	10	25	20
95	4	14	14
>100	16	67	12

† For trees <40 cm dbh, numbers and rates are determined from 4 ha of data. For trees >40 cm dbh, numbers and rates are determined from 20 ha of data.

‡ Stems crossing the 10 cm dbh threshold are recruited trees.

and with the reported trend of biomass accumulation in neotropical and Amazon forests (Phillips et al. 1998). Preliminary estimates of cumulative CO₂ flux from the eddy covariance measurements on the adjacent tower indicated loss of 0.7–2.0 Mg C·ha⁻¹·yr⁻¹ (data not shown), in close agreement with the biometric data presented here.

Sensitivity of results to CWD fluxes and pool size

The respiration from CWD, based on published decomposition rates measured in a forest near Manaus (Chambers et al. 2000, 2001b), represents the least-constrained parameter in the analysis of aboveground biomass flux. Nevertheless, net loss of carbon from CWD appears certain: decomposition rates would have to be only 0.05 yr⁻¹ for CWD to be in steady state at our site. This rate would be slower than in cold temperate forests (0.06 yr⁻¹; Turner et al. 1995).

The CWD budget might be closer to balance if inputs were larger than we derived from mortality rates, e.g., from large branch falls. Large branches commonly fall from live trees in the neotropics (Aide 1987, Chambers et al. 2001a); individual limbs as large as trees may fall, preferentially in previously created gaps (Young and Hubbell 1991). Most studies of limb loss focus on tree recovery following breakage (Putz and Brokaw 1989, Bellingham et al. 1994) or the effects of limb loss on the understory (Aide 1987, Clark and Clark 1989), and so the contribution of limb falls to CWD

remains uncertain. However, limb falls are unlikely to account for the imbalance in inputs and outflows in the pool of CWD, because associated inputs would have to equal or exceed mortality to bring the current CWD pool into balance. Note that falling limbs move carbon from live to dead pools, with no effect on our conclusion that carbon is being lost from combined aboveground pools.

A disturbance-recovery hypothesis to explain ecosystem carbon loss in the Tapajós Forest

What factors may be causing the net emission of (0.1–4.5 Mg C·ha⁻¹·yr⁻¹) of carbon from the site? Relevant features of the observations include:

- 1) Loss results from net emissions from CWD, which exceed the carbon accumulation in live trees (Table 2).
- 2) Accumulation in live biomass is concentrated in the small trees (Fig. 4a) and stem densities of smaller trees are also increasing (Fig. 4b).
- 3) Recruitment rates are very high ($4.8 \pm 0.9\%$), closer to rates observed in forest fragments (where baseline rates can be raised by up to ~70% [Laurance et al. 1998]) than in intact primary forest (0.81–2.8% [Phillips and Gentry 1994]).
- 4) Litter production is in the upper end of the range for neotropical forests.
- 5) The pool of CWD, the driver of carbon loss in this forest, is large not only by comparison to other forests, but also in comparison to mortality inputs. It would take ≈ 13 yr of the total input from mortality to accumulate just the excess CWD stock (above the steady state at present mortality input rates).

We propose a hypothesis that is consistent with all of these observed anomalies: that the site is in the process of recovery from a significant disturbance or disturbances which caused sharply elevated mortality in years preceding the onset of the study in 1999. This process would have caused the CWD pool to increase to the current state where losses substantially exceed inputs, and simultaneously opened canopy gaps. Canopy gaps stimulate recruitment of new trees, high levels of leaf production, and tree growth, causing the observed net accumulation in live biomass. If we are indeed observing the initial recovery phase, biomass accumulation would show up in smaller trees, as we have found.

The disturbance-induced mortality required to make this hypothesis work is significantly above background rates, but well below the near-complete mortality observed in large blow-downs (Nelson et al. 1994) that occur occasionally in the Amazon basin, apparently due to large convective storms (Garstang et al. 1998). Mortality rates of 5% yr⁻¹ (taken as the dividing line between background and catastrophic mortality by Lugo

and Scatena [1996]) would have to persist for ~ 4 yr to achieve current CWD pool sizes.

ENSO, drought in the Amazon, and its effects on net carbon flux

The protracted and severe droughts associated with the ENSO (El Niño Southern Oscillation) events in the 1990s (1992–1995, 1997–1998 Multivariate ENSO Index [MEI]⁸) could have contributed to a previous mortality event and the observed loss of carbon. El Niño years are associated with anomalously low rainfall over most of Amazonia (Ropelewski and Halpert 1987), and drought was particularly severe during the 1997–1998 ENSO, the strongest ENSO of the century (Marengo et al. 1998, McPhaden 1999, Williamson et al. 2000). Precipitation measured at Belterra, ~ 30 km from our site, shows strong drought conditions during the dry season (June to October) of 1997, when rainfall totaled 162.0 mm, compared to an average of 370.4 mm in non-ENSO years (data from Belterra weather station; E. Moran, *unpublished data*). Williamson et al. (2000) links such ENSO related drought to temporarily elevated tree mortality, reporting that when dry season rainfall near Manaus dropped to 232 mm during the 1997 ENSO, from the non-ENSO year average of 732 mm, tree mortality rates jumped from 1.12% to 1.91%. Other studies have shown increased tree mortality associated with ENSO events, though they do not cite drought conditions specifically (Leighton and Wirawan 1986, Condit et al. 1995, Kinnaird and O'Brien 1998).

The ENSO-induced mortality observed in these studies is less than the $\sim 5\%$ rate needed to explain our observations. It may be that the kilometer 67 site in the Tapajós Forest had a stand structure more susceptible to mortality than other forests, and this could have either made the ENSO effect bigger at this site, or could have contributed to a localized mortality event independent of ENSO. There is some evidence that the stand may be in a state of decline because of an advanced age structure, indicated by a greater tree density and a greater stand biomass at kilometer 67 (99.4 Mg C/ha) than at the nearby kilometer 83 site (88.5 Mg C/ha; Keller et al. 2001) for trees ≥ 35 . An advanced-age stand may be more likely to experience disturbance and elevated mortality because of biological limitations on tree size and stand structure. It has been observed that large trees (>70 cm dbh) are more drought susceptible (Clark and Clark 1996) than smaller trees.

Drought may also enhance CWD by slowing decomposition. Eddy-flux measurements at a nearby Tapajós Forest site indicate that dry conditions are linked to markedly lower ecosystem respiration (Goulden et al. 2004). Thus, the combination of increased input into the CWD pool by mortality with slower decomposition during the ENSO events of the 1990s could have caused

the accumulation of CWD pool that we observed, and the consequent emissions during the period of our study.

Model studies by Tian et al. (1998) suggested that undisturbed forests in the Amazon Basin should act as a source of CO₂ during dry El Niño years and a sink during other years (7.0×10^8 Mg C). In this study, we measured a carbon source in the years following a particularly strong ENSO event. We have suggested that the effect of recent ENSO events on the net carbon flux in this old-growth forest was delayed, leading to emissions well after the meteorological event. Lag in carbon budget response seems likely based on simple tree dynamics: mortality may occur within a year or two of an ENSO, but decomposition is actually inhibited during the event and in many cases takes 10–15 yr for large pieces of CWD. Carbon release is then more likely to occur when the drought ends. There may also be a “methodological” lag time associated with biometric measurements of carbon accretion from elevated recruitment, because trees must attain a minimum size class (in this study, 10 cm dbh) to be measured.

One might expect that, in the future, the forest will return to long-term net carbon balance as it recovers from an episode of drought and mortality. But if ENSO events increase in severity or frequency in response to changing climate, long-term carbon balance may be affected. Evidently, long monitoring periods are required to determine the contribution of this, or any, primary tropical forest to the budget of atmospheric CO₂.

Implications for biometric studies of forest carbon accumulation

The net uptake by live biomass in our Tapajós site, 1.40 ± 0.62 Mg C·ha⁻¹·yr⁻¹, is equal to the 90th percentile of uptake observed across all tropical forest plots in the Phillips et al. (1998) study. Nevertheless, the net carbon balance in the Tapajós for live and dead pools together is actually negative due to large respiration losses from an excess of CWD. Evidently, biometric studies of tropical forest carbon sequestration that neglect the CWD pool may be misleading, especially if study duration is shorter or comparable to the turnover time of CWD (on the order of 10 yr) or compared to the return frequency of important disturbance-inducing events such as ENSO.

These observations are generally relevant to ongoing studies of forest carbon sequestration. For example, the Phillips et al. study did not include CWD, yet their finding of statistically significant uptake in tropical systems depends on the inclusion of forest plots observed for less than 10 yr (Phillips et al. 1998, supplemental information); these plots (24 out of 68 plots globally) are precisely those most susceptible to the bias caused by excluding CWD. Detecting the effects of increasing atmospheric CO₂ on in situ tropical forest carbon se-

⁸ <http://www.cdc.noaa.gov/~kew/MEI/>

questration (a goal of an increasing number of studies) will also likely be difficult, since the predicted CO₂ fertilization signal (e.g., 0.42 Mg C·ha⁻¹·yr⁻¹ extra uptake [Tian et al. 2000]) is small compared to the signal we might expect from periodic climate-disturbance events (0.1–4.5 Mg C·ha⁻¹·yr⁻¹, taking the Tapajós as an indicator). Because climatic events such as ENSO are regional, the signal of climate-driven shifts in carbon balance may also be expected to extend broadly in space as well, suggesting that the need to include CWD may not be ameliorated even by spatially extensive sampling.

CONCLUSIONS

The present study shows net carbon loss from this old-growth tropical forest between 1999 and 2001, with accumulation in live biomass offset by even larger respiration losses from necromass. CWD was an especially large and labile pool of carbon with significant impact the net carbon budget for the ecosystem. This work shows that surveys of live biomass alone are insufficient to determine carbon budgets.

Several observations suggest that the site is recovering from a period of high mortality preceding the onset of the study: loss from necromass was due to an unusually large CWD pool, the net carbon accumulation observed in live biomass was concentrated exclusively in small size classes, and recruitment rates were much higher than what is typical for old-growth forests. We present the hypothesis that drought conditions resulting from the 1990s ENSO events (documented in local rainfall records) contributed to the elevated mortality that led, first, to a substantial transfer of biomass from live to dead pools and preservation of the dead pools during the dry periods, and subsequently (during our study), to both losses from CWD and gains in live biomass for smaller trees.

The observed loss of carbon (1.9 ± 1.0 Mg C·ha⁻¹·yr⁻¹) was large compared to the hypothesized carbon uptake from fertilization by elevated atmospheric CO₂ (0.42 Mg C·ha⁻¹·yr⁻¹ [Tian et al. 2000]), indicating that any signal from such uptake is likely to be strongly masked. Since ENSO events are regional, affecting tropical forests globally in different ways, interpretation of short-term ecological studies in terms of CO₂ fertilization should be approached with caution.

Climatic variations influence forest demographic processes, and thus carbon balance, for extended periods. For time scales of several years, a dominant signal in forest dynamics and net carbon budgets in this tropical forest, and no doubt in many others, appears to be climatic variation.

ACKNOWLEDGMENTS

This research was funded through NASA Grant NCC5-341 (LBA-Ecology) to Harvard University. We thank Bethany Reed, Lisa Zweede, Dan Hodkinson, Fernando Alves Leão, and the staff of the LBA-Santarém Office for their extensive

logistical support and patience; Nilson de Souza Carvalho and Ehrly Pedroso for sharing their invaluable knowledge and good humor in the field; Edna Tenório Guimarães for her leadership and persistence during implementation of the study; Franck Magalhães, George Macêdo, and Elder Campos for intensive field assistance; Nelson Rosa of the Museo Guedi, Belém for his expert botanical identifications; and Jeff Chambers and Carol Barford for valuable insights in planning and design.

LITERATURE CITED

- Aide, T. M. 1987. Limbfalls—a major cause of sapling mortality for tropical forest plants. *Biotropica* **19**:284–285.
- Anderson, J., and T. Spencer. 1991. Carbon, nutrient and water balances of tropical rain forest ecosystems subject to disturbance. United Nations Educational Scientific and Cultural Organization (UNESCO), Paris, France.
- Barford, C. C., S. C. Wofsy, M. L. Goulden, J. W. Munger, E. H. Pyle, S. P. Urbanski, L. Hutyrá, S. R. Saleska, D. Fitzjarrald, and K. Moore. 2001. Factors controlling long- and short-term sequestration of atmospheric CO₂ in a mid-latitude forest. *Science* **294**:1688–1691.
- Bellingham, P. J., E. V. J. Tanner, and J. R. Healey. 1994. Sprouting of trees in Jamaican montane forests, after a hurricane. *Journal of Ecology* **82**:747–758.
- Brown, I. F., L. A. Martinelli, W. W. Thomas, M. Z. Moreira, C. A. C. Ferreira, and R. A. Victoria. 1995. Uncertainty in the biomass of Amazonian forests: an example from Rondônia, Brazil. *Forest Ecology and Management* **75**: 175–189.
- Brown, J. K. 1974. Handbook for inventorying downed woody material. General technical report. USDA Forest Service, Ogden, Utah, USA.
- Brown, S. 1997. Estimating biomass and biomass change of tropical forests: a primer. United Nations Food and Agriculture Organization, Urbana, Illinois, USA.
- Brown, S., and A. E. Lugo. 1982. The storage and production of organic-matter in tropical forests and their role in the global carbon-cycle. *Biotropica* **14**:161–187.
- Brown, S., and A. E. Lugo. 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. *Interciencia* **17**:8–18.
- Chambers, J. Q., J. dos Santos, R. J. Ribeiro, and N. Higuchi. 2001a. Tree damage, allometric relationships, and above-ground net primary production in a central Amazon forest. *Forest Ecology and Management* **152**:73–84.
- Chambers, J. Q., N. Higuchi, J. P. Schimel, L. V. Ferreira, and J. M. Melack. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia* **122**:380–388.
- Chambers, J. Q., J. P. Schimel, and A. D. Nobre. 2001b. Respiration from coarse wood litter in central Amazon forests. *Biogeochemistry* **52**:115–131.
- Chave, J., B. Riera, and M. A. Dubois. 2001. Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *Journal of Tropical Ecology* **17**: 79–96.
- Clark, D. A. 2002. Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecological Applications* **12**:3–7.
- Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Thomlinson, J. Ni, and E. A. Holland. 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecological Applications* **11**: 371–384.
- Clark, D. B. 1996. Abolishing virginity. *Journal of Tropical Ecology* **12**:735–739.
- Clark, D. B., and D. A. Clark. 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest. *Oikos* **55**:225–230.

- Clark, D. B., and D. A. Clark. 1996. Abundance, growth, and mortality of very large trees in a neotropical lowland rain forest. *Forest Ecology and Management* **80**:235–244.
- Clark, D. B., and D. A. Clark. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management* **137**:185–198.
- Clark, D. B., D. A. Clark, S. Brown, S. F. Oberbauer, and E. Veldkamp. 2002. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. *Forest Ecology and Management* **164**:237–248.
- Condit, R., S. P. Hubbell, and R. B. Foster. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* **65**:419–439.
- Delaney, M., S. Brown, A. E. Lugo, A. Torres-Lezama, and N. B. Quintero. 1998. The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. *Biotropica* **30**:2–11.
- Dixon, R. K., S. Brown, R. A. Houghton, A. M. Solomon, M. C. Trexler, and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. *Science* **263**:185–190.
- Efron, B., and R. Tibshirani. 1997. Improvements on cross-validation: the .632+ bootstrap method. *Journal of the American Statistical Association* **92**:548–560.
- Fan, S., M. Gloor, J. Mahlman, S. Pacala, J. Sarmiento, T. Takahashi, and P. Tans. 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science* **282**:442–446.
- Franken, M. 1979. Major nutrient and energy contents of the litterfall of a riverine forest of central Amazonia. *Tropical Ecology* **20**:211–224.
- Garstang, M., S. White, H. H. Shugart, and J. Halverson. 1998. Convective cloud downdrafts as the cause of large blowdowns in the Amazon. *Meteorology and Atmospheric Physics* **67**:199–212.
- Gerwing, J. J., and D. L. Farias. 2000. Integrating liana abundance and forest stature into an estimate of total above-ground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology* **16**:327–335.
- Gillespie, A. J. R., S. Brown, and A. E. Lugo. 1992. Tropical forest biomass estimation from truncated stand tables. *Forest Ecology and Management* **48**:68–87.
- 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 CO₂ 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, 1992 to 1993. *Science* **270**:778–780.
- Gurney, K. R., et al. 2002. Towards robust regional estimates of CO₂ sources and sinks using atmospheric transport models. *Nature* **415**:626–630.
- Gut, A. 1995. *An intermediate course in probability*. Springer-Verlag, New York, New York, USA.
- Harmon, M. E., and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. Publication No. 20. U. S. Long-Term Ecological Research (LTER) Network Office, University of Washington, Seattle, Washington, USA.
- Hurttt, G. C., S. W. Pacala, P. R. Moorcroft, J. Caspersen, E. Shevliakova, R. A. Houghton, and B. Moore. 2002. Projecting the future of the US carbon sink. *Proceedings of the National Academy of Sciences (USA)* **99**:1389–1394.
- Keeling, R. F., S. C. Piper, and M. Heimann. 1996. Global and hemispheric CO₂ sinks deduced from changes in atmospheric O-2 concentration. *Nature* **381**:218–221.
- Keller, M., M. Palace, G. Asner, R. Pereira, Jr., J. N. M. da Silva. *In press*. Coarse Woody Debris in undisturbed and logged forests in the Eastern Brazilian Amazon. *Global Change Biology*.
- 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.
- Kinnaird, M. F., and T. G. O'Brien. 1998. Ecological effects of wildfire on lowland rainforest in Sumatra. *Conservation Biology* **12**:954–956.
- Klinge, H., and W. A. Rodrigues. 1968. Litter production in an area of Amazonian terra firme forest. Part I. Litter-fall, organic carbon and total nitrogen contents of litter. *Amazoniana* **1**:287–302.
- Laurance, W. F., L. V. Ferreira, J. M. Rankin-De Merona, S. G. Laurance, R. W. Hutchings, and T. E. Lovejoy. 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* **12**:460–464.
- Leighton, M., and N. Wirawan. 1986. Catastrophic drought and fire in Borneo tropical rain forest associated with the 1982–1983 El Niño Southern Oscillation Event. Pages 75–102 in G. T. Prance, editor. *Tropical rain forests and the world atmosphere*. Westview Press, Boulder, Colorado, USA.
- Lugo, A. E., and F. N. Scatena. 1996. Background and catastrophic tree mortality in tropical moist, wet and rain forests. *Biotropica* **28**:585–599.
- Luizao, F. J. 1995. *Ecological studies in contrasting forest types in central Amazonia*. University of Stirling, Stirling, Scotland, UK.
- Luizao, F. J., and H. O. R. Schubart. 1987. Litter production and decomposition in a terra-firme forest of central Amazonia. *Experientia* **43**:259–265.
- 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.
- Marengo, J. A., J. Tomasella, and C. R. Uvo. 1998. Trends in streamflow and rainfall in tropical South America: Amazonia, eastern Brazil, and northwestern Peru. *Journal of Geophysical Research-Atmospheres* **103**:1775–1783.
- Marston, J. B., M. Oppenheimer, R. M. Fujita, and S. R. Gaffin. 1991. Carbon-dioxide and temperature. *Nature* **349**:573–574.
- McPhaden, M. J. 1999. El Niño—the child prodigy of 1997–98. *Nature* **398**:559–562.
- Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore, C. J. Vorosmarty, and A. L. Schloss. 1993. Global climate-change and terrestrial net primary production. *Nature* **363**:234–240.
- Nelson, B. W., V. Kapos, J. B. Adams, W. J. Oliveira, O. P. G. Braun, and I. L. Doamaral. 1994. Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology* **75**:853–858.
- Nepstad, D., et al. 2002. The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. *Journal of Geophysical Research* **107**(D20), 8085 [doi: 10.1029/2001JD000360.]
- Parotta, J. A., J. K. Francis, and R. R. de Almeida. 1995. *Trees of the Tapajós: a photographic field guide*. General technical report IITF-1. United States Department of Agriculture, Rio Piedras, Puerto Rico.
- Phillips, O. L., and A. H. Gentry. 1994. Increasing turnover through time in tropical forests. *Science* **263**:954–958.

- Phillips, O. L., Y. Malhi, N. Higuchi, W. F. Laurance, P. V. Nunez, R. M. Vasquez, S. G. Laurance, L. V. Ferreira, M. 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. Changes in growth of tropical forests: evaluating potential biases. *Ecological Applications* **12**:576–587.
- Prentice, I. C., G. D. Farquhar, M. J. R. Fasham, M. L. Goulden, M. Heimann, V. J. Jaramillo, H. S. Keshgi, C. Le Quere, R. J. Scholes, and D. W. R. Wallace. 2001. The carbon cycle and atmospheric carbon dioxide. Pages 183–237 in J. T. Houghton, editor. *Climate change 2001: the scientific basis*. Cambridge University Press, Cambridge, UK.
- Prentice, I., and J. Lloyd. 1998. C-quest in the Amazon Basin. *Nature* **396**:619–620.
- Putz, F. E., and N. V. L. Brokaw. 1989. Sprouting of broken trees on Barro Colorado Island, Panama. *Ecology* **70**:508–512.
- Ropelewski, C. F., and M. S. Halpert. 1987. Global and regional scale precipitation patterns associated with El-Nino Southern Oscillation. *Monthly Weather Review* **115**:1606–1626.
- Schimel, D. S. 1995. Terrestrial ecosystems and the carbon-cycle. *Global Change Biology* **1**:77–91.
- Silver, W. L., J. Neff, M. McGroddy, E. Veldkamp, M. Keller, and R. Cosme. 2000. Effects of soil texture on below-ground carbon and nutrient storage in a lowland Amazonian forest ecosystem. *Ecosystems* **3**:193–209.
- Summers, P. M. 1998. Estoque, decomposicao, e nutrientes da liteira grossa em floresta de terra-firme, na Amazonia Central. *Ciencias de florestas tropicais*. Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil.
- Tans, P. P., I. Y. Fung, and T. Takahashi. 1990. Observational constraints on the global atmospheric CO₂ budget. *Science* **247**:1431–1438.
- Tian, H., J. M. Melillo, D. W. Kicklighter, A. D. McGuire, J. V. K. Helfrich, B. Moore, and C. J. Vorosmarty. 1998. Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* **396**:664–667.
- Tian, H., J. M. Melillo, D. W. Kicklighter, A. D. McGuire, J. Helfrich, B. Moore, and C. J. Vorosmarty. 2000. Climatic and biotic controls on annual carbon storage in Amazonian ecosystems. *Global Ecology and Biogeography* **9**:315–335.
- Turner, D. P., G. J. Koerper, M. E. Harmon, and J. J. Lee. 1995. A carbon budget for forests of the conterminous United States. *Ecological Applications* **5**:421–436.
- Van Wagner, C. E. 1968. Line intersect method in forest fuel sampling. *Forest Science* **14**:20–26.
- Williamson, G. B., W. F. Laurance, A. A. Oliveira, P. Delamonica, C. Gascon, T. E. Lovejoy, and L. Pohl. 2000. Amazonian tree mortality during the 1997 El Nino drought. *Conservation Biology* **14**:1538–1542.
- Young, T. P., and S. P. Hubbell. 1991. Crown asymmetry, treefalls, and repeat disturbance of broad-leaved forest gaps. *Ecology* **72**:1464–1471.