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 (54°58'W, 2°51'S) in order to assess carbon pool sizes, fluxes, and climatic controls on carbon balance. In 1999 there were, on average, 470 live trees ha^{-1} with diameter at breast height (DBH) ≥10 cm. The mean aboveground live biomass was 143.7 ± 5.4 Mg C ha^{-1}, with an additional 48.0 ± 5.2 Mg C ha^{-1} 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^{-1}), recruitment of new trees (0.63 ± 0.09 Mg C ha^{-1} yr^{-1}, reflecting a notably high stem recruitment rate of 4.8 ± 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 appear 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 CO_2 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

Carbon balance, biometry, Coarse Woody Debris, Tropical Forest, mortality, Carbon sequestration, Carbon release, El Niño, LBA

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 mid-latitudes (Tans et al. 1990, Fan et al. 1998, Gurney et al. 2002), possibly attributed to reforestation of abandoned agricultural lands and fire suppression (Hurtt et al. 2002). Ecosystem modeling studies (Tian et al. 1998, 2000; Prentice & Lloyd 1998) and some empirical studies (Phillips et al. 1998, Malhi et al. 1998, Grace et al. 1995) 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 Amazônia are typically uneven-aged with many large trees, indicating the long periods of succession assumed suitable for attaining carbon equilibrium (Anderson & 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 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 (Tian et al. 1998, Prentice & Lloyd 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-year or less) eddy-covariance studies of carbon exchange reported significant accumulation of carbon in two tropical forests, with net uptake of 1.1 to 5.9 Mg C ha^{-1} 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, inter-annual 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 ha^{-1} 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 inter-annual 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 & Gentry 1994, Clark & Clark 2000, Clark 2002); the significance of these potential methodological problems 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, Chambers et al. 2001a), thus changes in CWD can account for substantial carbon fluxes.

In this paper we report on the first 2+ 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°58'W, 2°51'S, Pará, Brazil), accessed by an entrance road at km 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 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 55m height), *Manilkara huberi* (Ducke) Chev., *Hymenaea courbaril* L., *Betholletia excelsa* Humb. & Bonpl., and *Tachigalia* spp., and a closed canopy at ~40m. 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 50m x 1000m transects were installed adjacent to the eddy-covariance tower in July of 1999 (Figure 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 (NE, E, and SE), while the fourth runs N-S, intersecting the E transect at 550 m. The long, continuous transects aim to incorporate spatial heterogeneity throughout the tower foot print, avoiding bias associated with small scattered plots which 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 10m by 1000m, for a total area 3.99 ha) running down the middle of the larger transects. Whole-sample measures reported on an areal basis (stems per ha, growth rate per ha, etc) were calculated as a per-area weighted sum of small (10cm < DBH < 35cm) and large tree (≥35 cm DBH) samples. Trees with significant buttresses were measured above buttress termination.

Stainless steel dendrometer bands were placed on a random sub-sample of 1000 trees, stratified by taxonomic family and size class, in December 1999 (Table 1). The 48 identified taxonomic families were divided into 5 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 & 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 sub-groups that have more limited influence on carbon balance. We banded a large number of trees 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 "sub-canopy", 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 to 6 weeks 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. DBH of the 1000 sub-sampled trees with dendrometers were remeasured in April of 2001, while the DBH of remaining non-banded trees were remeasured in July of 2001, providing a 2 year growth increment for trees that survived the sampling interval. The April 2001 DBH resurvey of banded trees was adjusted to the full two-year interval by adding 3 months (April-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 10cm 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 (equations 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 pair-wise 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 percent of the frequency distribution of growth rates (i.e., trees with growth rates < -4.8 cm yr^{-1} or >5.3 cm yr^{-1}, 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 Mg C ha^{-1} yr^{-1}) by the following sum:

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

where Δt is the sampling interval, d_i is the observed stem density from the original inventory (trees ha^{-1}) and $\overline{\Delta B_i}$ is the measured mean biomass increment in the dendrometry subsample (Mg C tree^{-1}), 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 re-survey 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 10cm + g_{99}, where g_{99} is the 99th percentile of the 2-year 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. DBH measurements of standing dead trees were used to find an estimate of top diameter using Chambers et al. (2000) taper function and then were converted to volumes using the formula for a frustum of a cone (Harmon & Sexton 1996). In July 2001, we made dimensional measurements of fallen CWD in a series of nested plots within the 19.75 ha used for live biomass measurements (Table 1, Figure 1). All fallen debris greater than 30 cm in diameter and 1m in length were tagged, measured and assigned to decay classes in thirty-two 20 x 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 x 5 m subplots, and all debris from 2 to 10 cm were measured in 64 1 x 1 m subplots, randomly located within the 5m by 5m plots (Figure 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.

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 & 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 km 83, 17 km south of the site described here). For CWD greater than 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 1 of 8 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 - 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. (2003).

For comparison, necromass was also estimated using wood density numbers from other tropical forests in Clark et al. (2002), Delaney et al. (1998) and Summers (1998). 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 km 67 site using the line intercept method (Van Wagner 1968, Brown 1974, Table 1). In January 2002, 2000 m of line were run, in 10 m segments, measuring pieces greater than 10 cm in diameter and 400 m of line, in 10m segments, measuring pieces greater than 2 cm in diameter. The line intercept survey estimates of CWD volumes (~ 164 m^3 ha^{-1}) agreed with the plot based estimates (~ 152 m^3 ha^{-1}), within sampling uncertainty (1000 bootstrap simulations, using each individual CWD line segment as the 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 (Table 2b, Table 4).

To examine change in the stock of the CWD pool, we compared measured mortality inputs (methods above) to CWD respiration losses. We estimated these losses by assuming respiration follows first-order kinetics, respiration = $k \cdot$ (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 $k = 10^{((-1.788 \pm 0.27(SE)) \cdot \rho)} = \exp((-4.117 \pm 0.62(SE)) \cdot \rho)$, derived from CWD respiration studies in tropical forest near Manaus, Brazil (Chambers et al., 2001b), and from our decay class specific densities, ρ (Table 4). 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: $\bar{k} = \exp(-4.117 \cdot \rho + ½ (0.62 \cdot \rho)^2)$ (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 $k = 0.17\ yr^{-1}$, from a study of CWD mass-loss over 10-15 years in a tropical forest near Manaus (Chambers et al. 2000). Lower bound $k=0.0825\ yr^{-1}$, based on an average across non-pine temperate forests (oak-hickory, and bottomland hardwoods) in the southern U.S. (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 mid-latitude 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, see section further below) 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 m^2) randomly located throughout the 19.75 ha tree survey area. Every two weeks, 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; (4) miscellaneous. We report here on the 19-month period from July 2000 through February 2002.

Uncertainty Analysis

We quantified two kinds of uncertainties in general: sampling uncertainty, and uncertainties due to non-statistical 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 & Tibshirani, 1997), and non-statistical 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 50m long as the unit of replication for recruitment. 95% confidence intervals are reported as central estimate (± uncertainty) unless otherwise indicated. For brevity and a more conservative analysis, asymmetrical confidence limits (as with distributions that are log-normal) 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 *Resp* =

$k \cdot CWD_{mass} = exp(b \cdot \rho) \cdot (CWD_{vol} \cdot \rho)$, where CWD_{vol} was the volume of the sample piece, b was drawn from its normal distribution (mean = -4.117, 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 (versus 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=2 standing dead snags in Chambers et al, 2001b), so we used a simple approach that assumed all standing CWD respires 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 ha^{-1}, respectively. The total aboveground live biomass was 143.7 ±5.4 Mg C ha^{-1} in 1999 and 147.4 ±5.9 Mg C ha^{-1} 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 (Chave et al. 2001, Keller et al. 2001, Brown et al. 1992, Brown et al. 1995, Gerwing & Farias 2000). However, live biomass for trees ≥35 DBH (99.4 Mg C ha^{-1}) was 12% greater than a nearby Tapajós survey reporting 88.5 Mg C ha^{-1} of biomass (Keller et al. 2001). Allometric uncertainty for standing biomass was about the same as sampling uncertainty, each less than ±10% (Table 2a). Larger trees (≥35 cm DBH) accounted for the main portion of total biomass (67%), though smaller trees (≥10 cm & < 35 cm DBH) were much more common (1780 trees, 64% of stems).

The distribution of stem density vs. size was piecewise log-linear with a distinctly steeper slope for trees < 40 cm DBH (Figure 2). The size class at which the slope change occurs is about the same as the cut-off 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 sub-transects (on which all trees ≥10cm were inventoried) was indistinguishable from Figure 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 log-linear 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 ha^{-1} yr^{-1} (n = 2561 trees, Table 2a) based on 1999 and 2001 DBH measurements, a mean diameter increase of 0.36 cm yr^{-1}. The diameter growth increment per-tree increased with size until 40 cm DBH (Figure 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 (Figure 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 ha^{-1} yr^{-1} for trees < 35 cm DBH, Figure 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 to 3.1 Mg C ha^{-1} 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 (Figure 5a).

Trees were recruited at a rate of 23 ha^{-1} yr^{-1}, adding 180 new stems and 0.63 ± 0.09 Mg C ha^{-1} yr^{-1} to our pool of aboveground live biomass (Table 2a, Figure 6). Stem recruitment rates (4.8 ± 0.9%) were elevated compared to rates for other undisturbed forests in the central Amazon, which average 1.84% (Laurance et al. 1998, corrected to 2 year sampling interval) with a range of 0.81 – 2.32% (Phillips & 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 re-survey, 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 anomolusly high. We observed that the rate of trees crossing into the 10-15cm size class was not detectably different from the rate of trees crossing into other 5cm size-class intervals (Table 3), 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; Figures 4a and 6) offsets accumulation of aboveground live biomass through growth and recruitment. Eighty-eight trees died in the two-year 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 10^{th} and 90^{th} percentiles for both (Lugo & 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) (Figure 4a, 4b). The contrast with carbon gain in live biomass (dominated by smaller trees) is discussed below.

Dividing the live biomass pool by input (growth +recruitment) or outflow (mortality) gave turnover times of 38 and 59 years, respectively, whereas the stem turnover times, based on 4.8 ± 0.9% recruitment and 1.7% mortality, were 21 and 59 years (geometric mean 31 years). The stem turnover times are shorter than for other Amazonian forests: average turnover from mortality was 67 years for twelve Amazonian sites (Lugo & Scatena, 1996) and 80 years (geometric mean of mortality and recruitment turnover times) for five other Amazonian sites (Phillips & Gentry 1994). Our site in the Tapajós is more dynamic than other Amazonian forests, this is possibly a response to a recent disturbance (see below).

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 (Figure 6) to the net flux measured in an aggrading temperate forest in central Massachusetts (Harvard Forest, Barford et al. 2001; see Figure 6), despite the much larger gross fluxes in Tapajós.

Figure 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 to 85 cm) trees, mortality outstrips growth and recruitment (Figure 4a). Stem density increased from 448 to 478 trees ha^{-1} (1.44 Mg C ha^{-1} yr^{-1} biomass accumulation) in classes < 60 cm but was essentially stable (from 20 to 19 trees ha^{-1}, 0.04 Mg C ha^{-1} yr^{-1} biomass loss) in classes ≥ 60 cm (Figure 4).

Coarse Woody Debris: Pool sizes and Fluxes

CWD totaled 48.0 ± 5.2 Mg C ha^{-1} with a large fraction (18%, or 27 stems ha^{-1}) as standing dead snags (Table 4b). CWD estimates using wood densities derived in other neotropical forests gave slightly lower numbers: 31.9 ± 3.6 Mg C ha^{-1}, 40.4 ± 5.2 Mg C ha^{-1} and 42.8 ± 4.5 Mg C ha^{-1} (Clark et al. 2002, Delaney et al. 1998, Summers 1998, respectively). CWD exhibited high spatial variability (e.g. 6-fold differences in average volume across the 16 large CWD plots in Figure 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^{-1} 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^{-1} for fallen pieces ≥2 cm), Clark et al. (2002) (23 Mg C ha^{-1} for pieces ≥ 10 cm), and Brown et al. (1995) (15 Mg C ha^{-1} ≥ 10 cm). Total CWD ≥10 cm (44.0 Mg C ha^{-1}) was significantly higher than Summers (1998) estimate of 32.3 Mg C ha^{-1} for a nearby forest in Manaus. There is also evidence that the CWD at km 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 m^3 ha^{-1}) and the line-intercept method (164.2 ± 38.1 m^3 ha^{-1}) are both ~50% higher than in the nearby forest at km 83 (109 m^3 ha^{-1} by line-intercept, data not shown). Note that our forest at km 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 4a), 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 to 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≥10cm 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 two-year 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.

Fine Litter: Pool size and Flux

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

Rodrigues 1968, Brown & 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.

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 $F=43.7$, $p<0.0001$; year $F=25.5$, $p<0.0001$). Suppressed and sub-canopy trees grew at significantly smaller rates than canopy and emergent trees, and growth in the wet year (Feb 2000 – Feb 2001, precip =2,412 mm) significantly exceeded the dry year (Feb 2001 – Feb 2002, precip = 1805 mm) growth (Figure 5a). Precipitation also correlated with tree growth at the monthly time scale (pearson correlation coefficient, $r = +0.71$, $p<.001$; Figure 5b). Litterfall also correlated with rainfall, but in the opposite sense (biweekly litterfall versus precip correlation, $r = -0.4$, $p<.01$) (Figure 5b).

DISCUSSION

Aboveground biomass measurements for the two-year study period indicate net emission of carbon from this site (1.9 ± 1.0 Mg C ha^{-1} yr^{-1}), an apparent contrast with both the eddy-covariance studies that report net carbon uptake in similar Amazonian forests (Malhi et al. 1998, Grace et al. 1995), and with the reported trend of biomass accumulation in neotropical and Amazon forests (Phillips et al., 1998). Preliminary estimates of cumulative CO_2 flux from the eddy covariance measurements on the adjacent tower indicated loss of 0.7 to 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, Chambers et al. 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 & Hubbell, 1991). Most studies of limb loss focus on tree recovery following breakage (Bellingham et al. 1994, Putz & Brokaw 1989) or the effects of limb loss on the understory (Aide 1987, Clark & 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:

- Loss results from net emissions from CWD, which exceed the carbon accumulation in live trees (Table 2).
- Accumulation in live biomass is concentrated in the small trees (Figure 4a) and stem densities of smaller trees are also increasing (Figure 4b).
- Recruitment rates are very high (4.8 ± 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 & Gentry, 1994).
- Litter production is in the upper end of the range for neotropical forests.
- 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 years 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 & Scatena 1996) would have to persist for about 4 years 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 1990's (1992-95, 1997-98; see http://www.cdc.noaa.gov/~kew/MEI/, ' Multivariate ENSO Index (MEI)') 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 Amazônia (Ropelewski & Halpert 1987), and drought was particularly severe during the 1997-1998 ENSO, the strongest ENSO of the century (Williamson et al. 2000, Marengo et al.1998, McPhaden 1999). Precipitation measured at Belterra, about 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 (EMBRAPA 1999). 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 (Kinnaird & O'Brien 1998, Leighton & Wirawan 1986, Condit et al. 1995).

The ENSO-induced mortality observed in these studies is less than the ~5% rate needed to explain our observations. It may be that the km 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 km 67 (99.4 Mg C ha^{-1}) than at the nearby km 83 site (88.5 Mg C ha^{-1}, 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 & 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, this issue). 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 CO_2 during dry El Niño years and a sink during other years (+7.0 $\cdot 10^8$ 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 case takes 10-15 years 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 CO_2.

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 (of order 10 years) 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 years (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 CO_2 on in situ tropical forest carbon sequestration (a goal of an increasing number of studies) will also likely be difficult, since the predicted CO_2 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 typical for old-growth forests. We present the hypothesis that drought conditions resulting from the 1990's 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 CO_2 (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 CO_2 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.

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Table 1: Measurements of biomass pools and fluxes at km 67, Tapajós National Forest

Pool or Flux	Measurement Method	Size Class	area	n =	frequency
Live above ground biomass	DBH survey	> 35 cm DBH	19.75 ha	~1000 stems	2 years
	DBH survey	10 - 35 cm DBH	3.99 ha	~1800 stems	2 years
Growth Increment	DBH comparison	> 35 cm DBH	19.75 ha	951 stems	2 years
	DBH Comparison	10 - 35 cm DBH	3.99 ha	1610 stems	2 years
	Dendrometers	> 10 cm DBH	19.75 ha	1000 stems	6 weeks
Mortality	DBH survey	> 35 cm DBH	19.75 ha	30 stems	2 years
	DBH survey	10 - 35 cm DBH	3.99 ha	57 stems	2 years
Recruitment	DBH survey	10 - 35 cm DBH	3.99 ha	201 stems	2 years
Standing CWD	Stem survey	> 10 cm DBH	19.75 ha	539 snags	once
Fallen CWD	Plot-based survey	> 30 cm diameter	32x120m^2 plots	246 pieces	once
	Plot-based survey	10 - 30 cm diameter	64x25m^2 plots	191 pieces	once
	Plot-based survey	2 - 10 cm diameter	64x1m^2 plots	390 pieces	once

Fallen CWD	Line-intercept survey	> 10 cm diameter	200 x 10m lines	249 pieces	once
	Line-intercept survey	2- 10 cm diameter	40 x 10m lines	238 pieces	once
Litter fall	Litter traps	< 2 cm diameter	40 x 0.43 m^2	-	2 weeks

Table 2: Aboveground biomass pool sizes and fluxes between July 1999 and July 2001 (all uncertainties are ± 95% confidence intervals)

Pool or Flux (n= number of stems)	Best estimate*	Alternate A†	Alternate B‡
A. LIVE BIOMASS			
(i) Pool size(Mg C ha^{-1}), in trees > 10 cm DBH			
1999 (n= 2648)	143.7 (± 5.4)	154.4 (± 9.0)	161.4 (± 11.1)
2001 (n=2803)	147.4 (± 5.9)	157.9 (± 8.8)	164.5 (± 12.0)
(ii) Fluxes to aboveground live biomass (Mg C ha^{-1} yr^{-1}), in trees > 10 cm DBH			
Recruitment (n= 180)	0.63 (± 0.09)	0.53 (± 0.08)	0.53 (± 0.08)
Growth (n= 2561)	3.18 (± 0.20)	3.25 (± 0.22)	3.11 (± 0.28)
Mortality (n= 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			
(i) Pool size ($Mg\ C\ ha^{-1}$), standing (>10 cm DBH) and fallen (>2 cm pieces)			
	48.0 (± 5.2)	NA	NA
(ii) Fluxes to CWD, $Mg\ C\ ha^{-1}\ yr^{-1}$			
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)			
(i) Pool size, $Mg\ C\ ha^{-1}$	195.4 (± 7.9)	205.9 (± 9.8)	212.5 (± 13.1)
(ii) Net Flux, $Mg\ C\ ha^{-1}\ yr^{-1}$	-1.9 (± 1.0)	(range: -0.1 to –4.5) §	

* "Best estimate" 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 4a). Allometry is: $Ln[Tree\ mass] = -1.06 + 0.333 \cdot Ln(DBH) + 0.933 \cdot Ln(DBH)^2 - 0.122 \cdot Ln(DBH)^3$, with DBH in cm and tree mass in kg C in biomass (assuming 1 kg dry biomass = 0.5 kg C biomass).

† "Alternate A" values are derived using Brown (1997) universal tropical allometry (eqn. 3.2.3) for tree biomass, and a lower-bound CWD respiration rate constant of $k = 0.0825\ yr^{-1}$, the average of respiration rates across non-pine forests in the southern U.S. (Turner et al., 1995). Allometry is: $Tree\ mass = 21.345 - 6.4 \cdot (DBH) + 0.621 \cdot (DBH)^2$

[‡] "Alternate B" values are derived using Brown (1997) universal tropical allometry (eqn. 3.2.4) for tree biomass, and an upper-bound respiration rate constant of $k = 0.17\ yr^{-1}$ for CWD respiration. Allometry is: *Ln[Tree mass] = –2.827 +2.53·Ln·(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: The number of stems crossing a size class threshold (every 5 cm) verses the number of stems originally in a size class, expressed as raw numbers and as an annualized percent rate.

Threshold	Stems crossing threshold	Stems originally present in size class	Percent rate of stems crossing threshold -------%yr-1-------
10[A]	201[B]	882	11%
15	78	419	9%
20	36	192	9%
25	21	92	11%
30	19	61	16%
35	11	32	17%
40[C]	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%

[A] For trees < 40 cm DBH, numbers and rates are determined from 4 ha of data; [B] Stems crossing the 10 cm DBH threshold are recruited trees; [C] For trees > 40 cm DBH, numbers and rates are determined from 20 ha of data

Table 4. (a) Coarse woody debris densities, respiration rates, pool-sizes, and respiration, by decay class.

Decay class	Density	k *	Volume		Mass	Respiration
			Fallen	Standing		
	Mg biomass/m^3	$Year^{-1}$	--------- m^3 ha^{-1} --------		Mg C ha^{-1}	Mg C ha^{-1} yr^{-1}
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: †						5.7 (±1.0)

* Decay-class specific CWD respiration rate derived from $k = \exp(b \cdot \rho)$, where b = -4.117± 0.62 (SE), ρ= density (Chambers et al., 2001b), and an unbiased estimate of mean *k* assuming normal distribution of the exponent is $\overline{k} = \exp(-4.117 \cdot \rho + \frac{1}{2} (0.62 \cdot \rho)^2)$ (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 respires 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}).

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

CWD Size class (number of pieces)	Volume fallen CWD	+	Volume standing CWD	=	Volume total CWD	Mass
			---------- m3 ha^{-1} (95% C.I.) ---------			-Mg C ha-1((± 95% C.I.)-
>30 cm (n=456)	97.7 (±14.7)	+	31.6 (±6.3)	=	129.4 (±17.6)	33.9 (±5.2)
10-30 cm (n=520)	34.6 (±5.8)	+	2.6 (±0.2)	=	37.3 (±7.3)	9.4 (±1.5)
2-10 cm (n=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)

Figure Captions

Figure 1: Map of transects and CWD plots for km 67 site in the Tapajós National Forest, Brazil.

Figure 2: Stem density (trees ha^{-1}, log scale) vs. DBH for the 2001 live biomass survey. Two different log-linear trend lines were fit to data for trees > and < 40 cm DBH (estimated regression coefficients ± standard errors are shown).

Figure 3: Average annual growth increment per tree (cm $tree^{-1}$ yr^{-1}) and annual biomass increment per tree (Mg biomass $tree^{-1}$ yr^{-1}), by size class [a]. Growth increment per tree increases with size up to 40 cm DBH; above 40 cm DBH there is no discernable pattern because of large error bars due to small samples sizes.

[a] Biomass increment calculated using Chambers et al. (2001a) allometry.

Figure 4:

(a) Gross fluxes to aboveground live biomass[a] , by size class, due to growth, mortality, and recruitment[b] (black and hatched bars), and corresponding net flux (gray bars) showing carbon accretion in small size classes and carbon loss from larger size classes.

[a] Allometry from Chambers et al. 2001a, [b] Recruitment for the smallest size class were "grow-ins" or previously unsurveyed stems, in subsequent classes, trees which grew across size class limits were added into the new size class ("ingrowth"), and subtracted from the preceding class as "outgrowth."

(b) Gross changes in tree stem density (trees ha^{-1}), by size-class, due to ingrowth, mortality, and outgrowth (black and hatched bars), and corresponding net changes in stem density (gray bars).

Figure 5: (a) Mean tree growth increment (± 95% C.I.), 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 [a]: 2200 mm in 2000, 1846 mm in 2001). Mean DBH in 2001 in each canopy status category are indicated by text overlay.

(b) Growth fluxes to aboveground tree biomass (February 2000 – July 2002)[b] and in litterfall (July 2000 – July 2002), together with biweekly precipitation.[a] (Flux-precipitation correlations are: tree growth: $r = +0.71$, $p<.001$; litterfall: $r = -0.4$, $p<.005$)

[a] Precipitation data from Nepstad et al. 2002

[b] Biomass increment calculated using Chambers et al. (2001a) allometry.

Figure 6: Gross and net fluxes to live, dead and total aboveground biomass in the Tapajós National Forest and in a temperate mid-latitude forest (Harvard Forest, Petersham, MA). 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.

Figure 1:

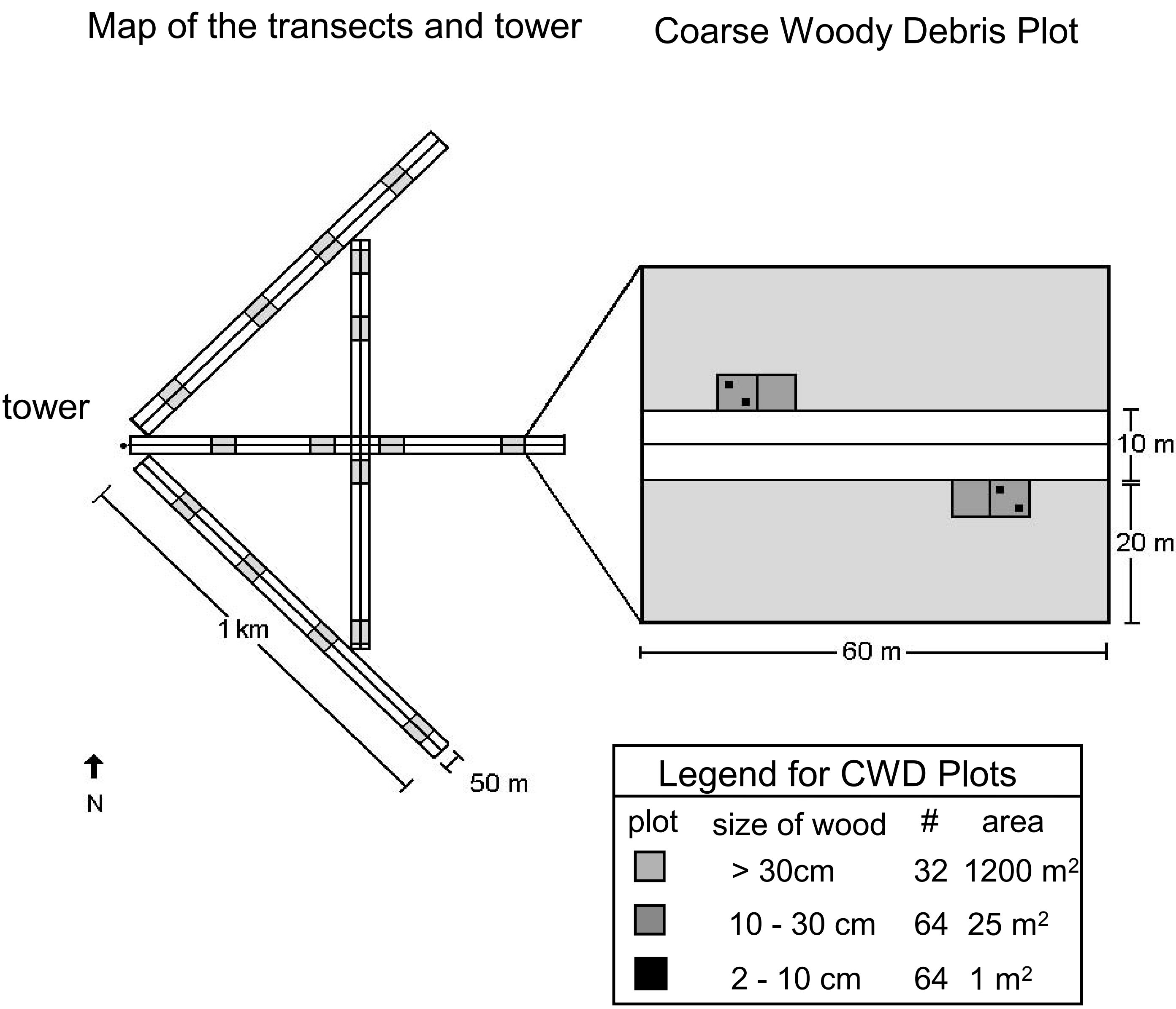
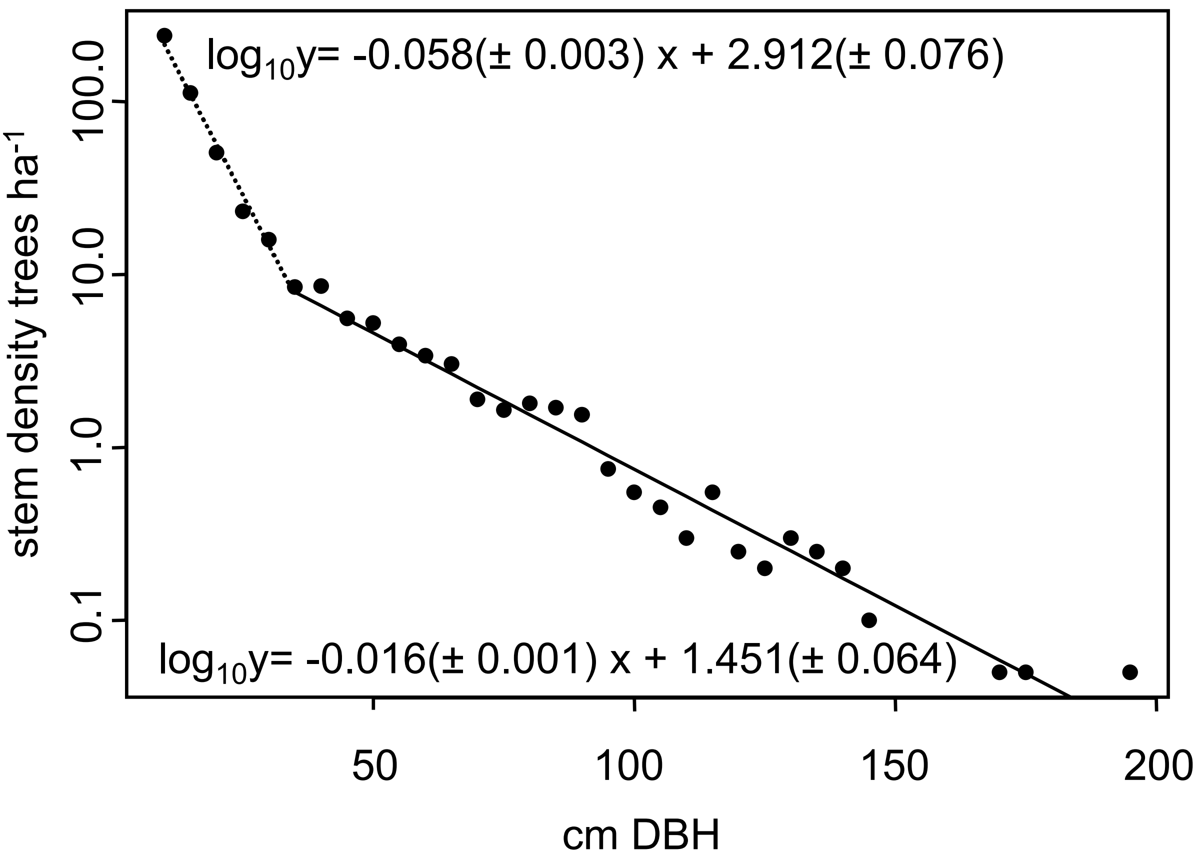
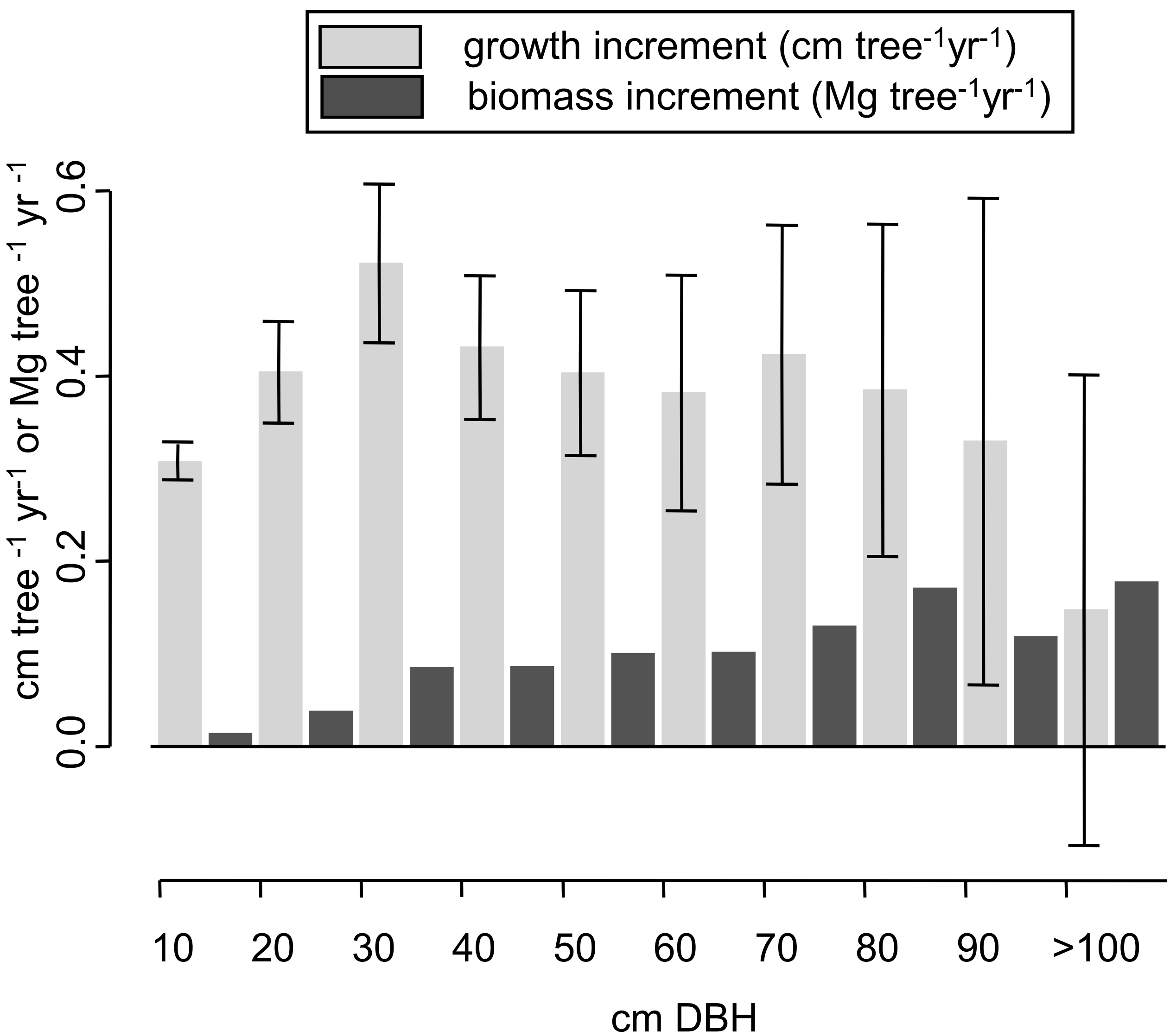

Map of the transects and tower
Coarse Woody Debris Plot
tower
1 km
50 m
N
10 m
20 m
60 m
Legend for CWD Plots
plot
size of wood
#
area
> 30cm
32
1200 m²
10 - 30 cm
64
25 m²
2 - 10 cm
64
1 m²

Figure 2:



log10y= -0.058(± 0.003) x + 2.912(± 0.076)
log10y= -0.016(± 0.001) x + 1.451(± 0.064)
stem density trees ha-1
100.0
10.0
1.0
0.1
50
100
150
200
cm DBH

Figure 3:



growth increment (cm tree-1yr-1)
biomass increment (Mg tree-1yr-1)
cm tree -1 yr-1 or Mg tree -1 yr -1
0.0
0.2
0.4
0.6
10
20
30
40
50
60
70
80
90
>100
cm DBH

Figure 4:

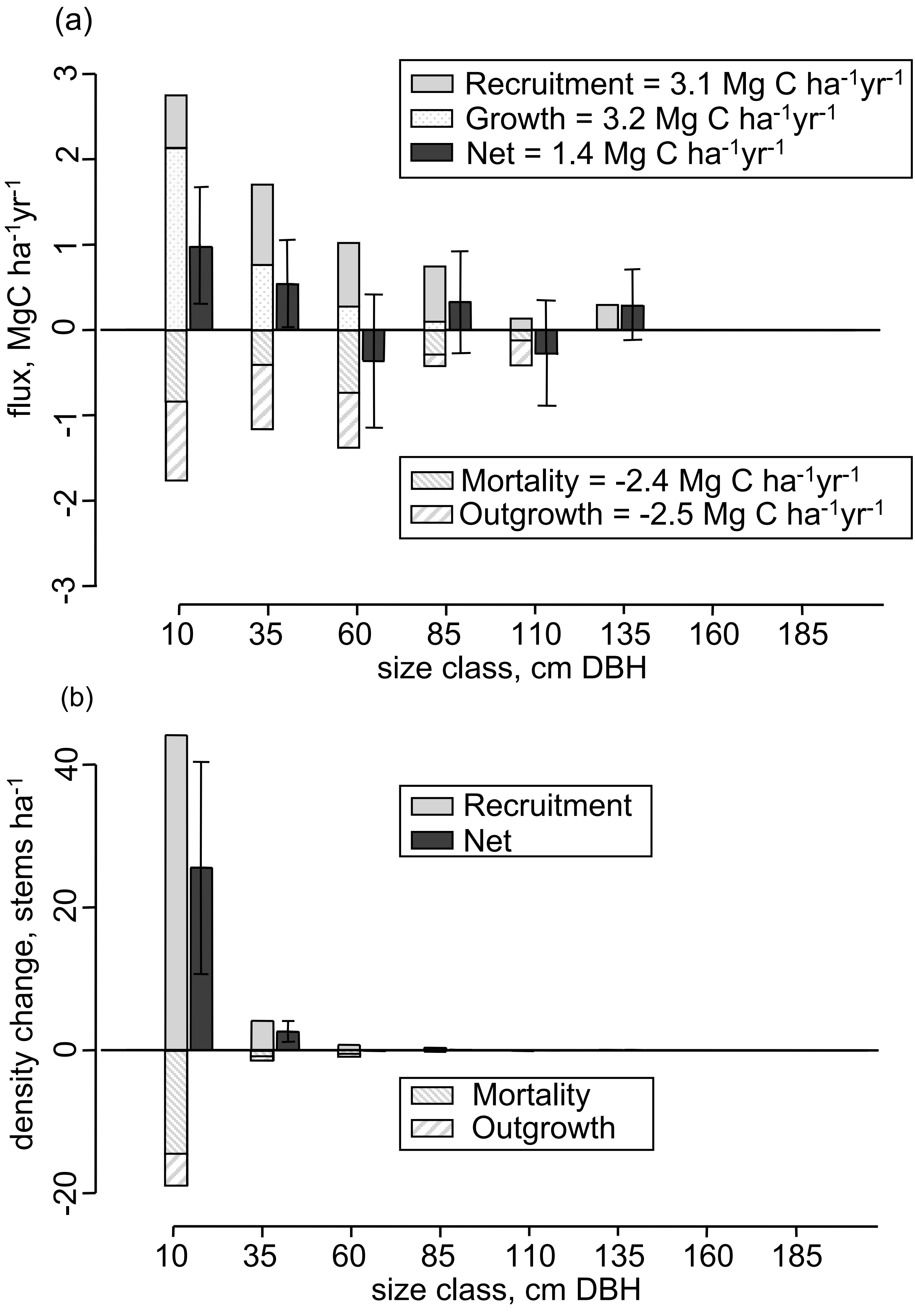
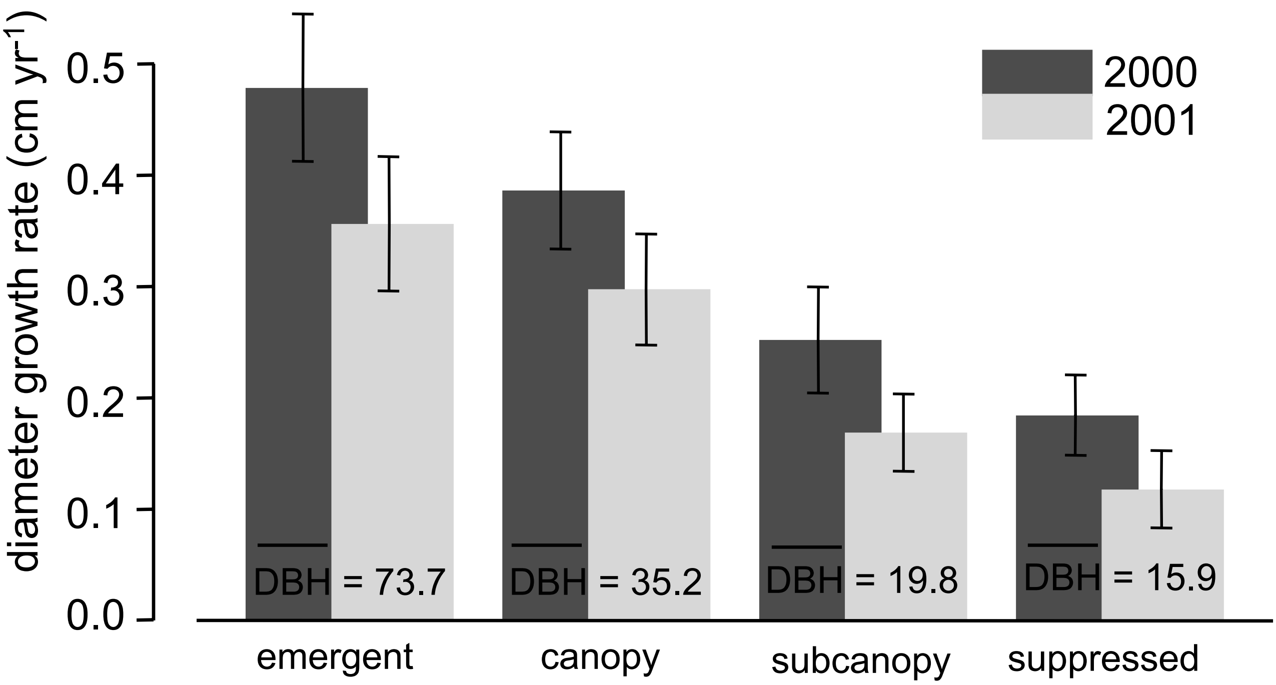

(a)
Recruitment = 3.1 Mg C ha-1yr-1
Growth = 3.2 Mg C ha-1yr-1
Net = 1.4 Mg C ha-1yr-1
Mortality = -2.4 Mg C ha-1yr-1
Outgrowth = -2.5 Mg C ha-1yr-1
flux, MgC ha-1yr-1
3
2
1
0
-1
-2
-3
10
35
60
85
110
135
160
185
size class, cm DBH
(b)
Recruitment
Net
Mortality
Outgrowth
density change, stems ha-1
40
20
0
-20
10
35
60
85
110
135
160
185
size class, cm DBH

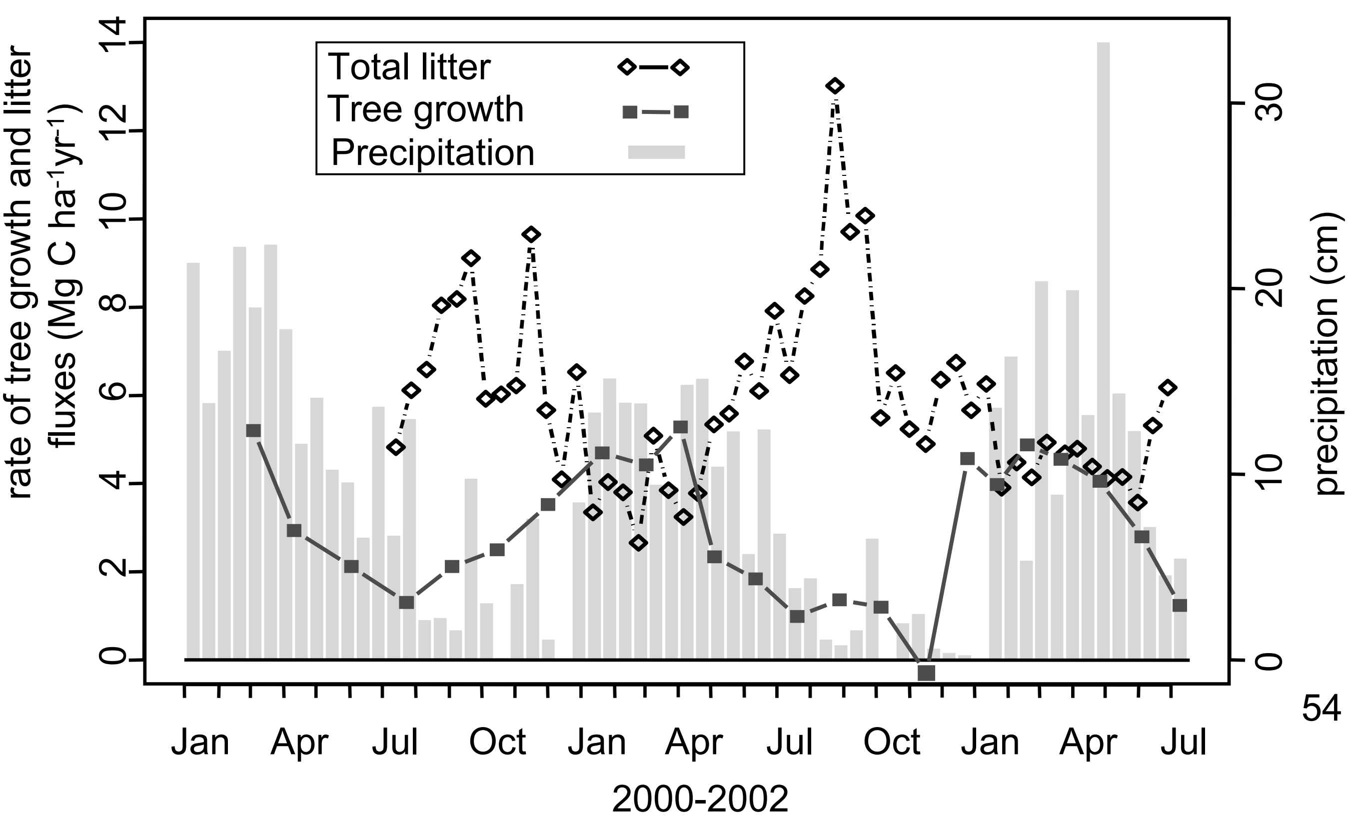
Figure 5:

(a)



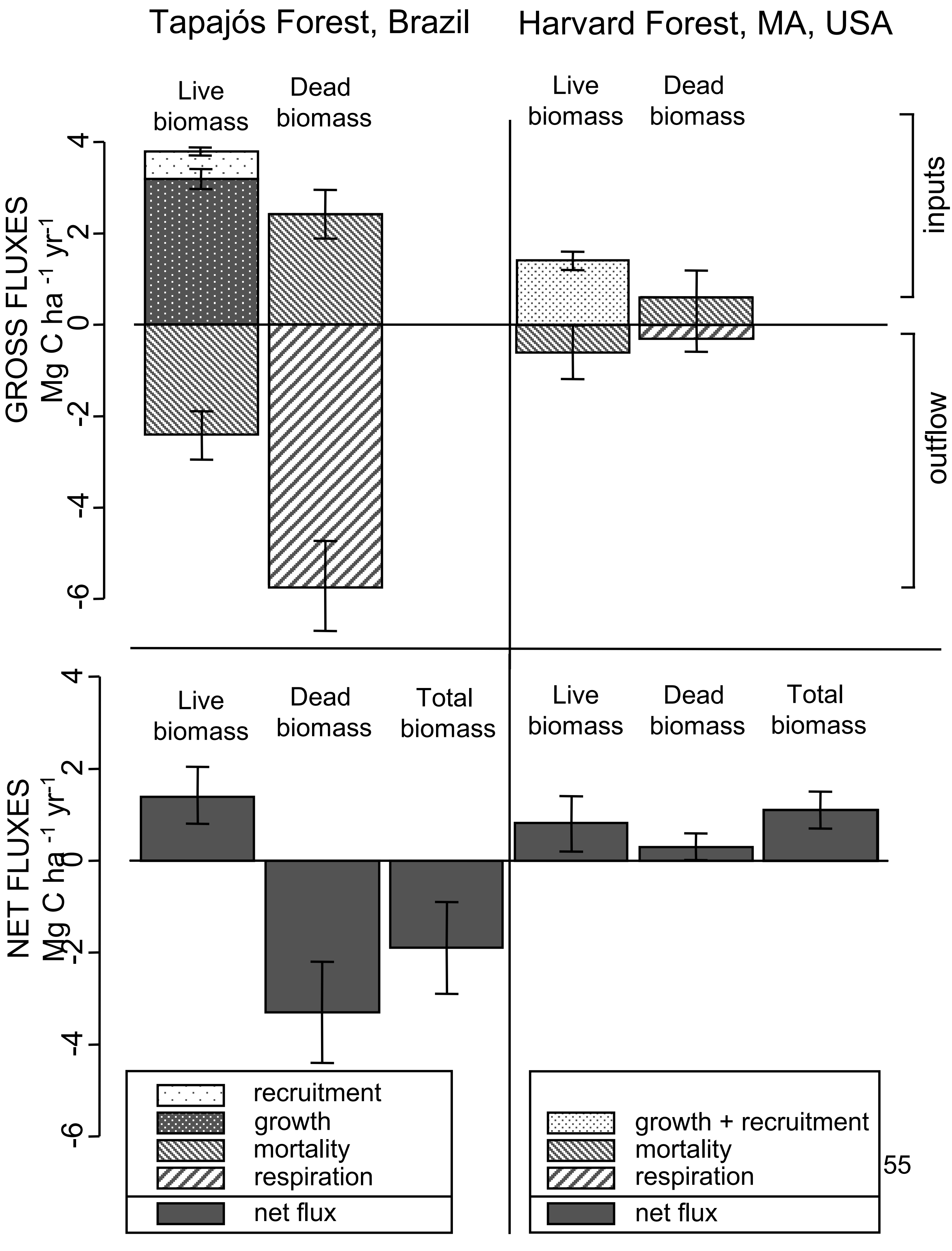
diameter growth rate (cm yr-1)
0.0
0.1
0.2
0.3
0.4
0.5
2000
2001
DBH = 73.7
DBH = 35.2
DBH = 19.8
DBH = 15.9
emergent
canopy
subcanopy
suppressed

(b)



rate of tree growth and litter fluxes (Mg C ha-1yr-1)
0
2
4
6
8
10
12
14
Total litter
Tree growth
Precipitation
precipitation (cm)
0
10
20
30
Jan
Apr
Jul
Oct
Jan
Apr
Jul
Oct
Jan
Apr
Jul
2000-2002

Figure 6:



Tapajós Forest, Brazil
Harvard Forest, MA, USA
GROSS FLUXES
Mg C ha -1 yr-1
Live biomass
Dead biomass
Live biomass
Dead biomass
inputs
outflow
4
2
0
-2
-4
-6
NET FLUXES
Mg C ha -1 yr-1
Live biomass
Dead biomass
Total biomass
Live biomass
Dead biomass
Total biomass
4
2
0
-2
-4
-6
recruitment
growth
mortality
respiration
net flux
growth + recruitment
mortality
respiration
net flux