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Short-Term Temporal Changes in Tree Live Biomass in a Central Amazonian Forest, Brazil

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ABSTRACT

We monitored seventy-two 1 ha permanent plots spread over 64 km^2 of *terra firme* forest at Reserva Ducke (Manaus, Amazonas, Brazil) over 2-yr intervals to assess the effects of a soil and topographic gradient on the rate of change in the aboveground tree live biomass (AGLB). AGLB increased significantly over the 2-yr intervals, exhibiting a mean rate of change of 1.65 Mg/ha/yr (bootstrapped 95% CI: 1.15, 2.79). The rate of change varied according to tree size class; understory and sub-canopy trees exhibited higher rates of change. Over the whole period, the rate of change was not related to soil or topographic features of the plots, but there was evidence that the relationships varied depending on the year of measurement. In the plots monitored between 2001 and 2003 we found a significant relationship between AGLB change and the soil textural gradient, but this relationship was not evident in plots monitored between 2002 and 2004. This suggests that both the temporal variation in the soil–biomass change relationship and the size structure of the forest need to be included in models of biomass change in Amazonia. We also noted that the rate of biomass change is sensitive to the equation used to estimate AGLB. Allometric models that incorporate wood-density data provide higher per plot AGLB estimates, but lower rates of change, suggesting that variations in floristic composition have important implications for carbon cycling in diverse tropical forests.

Abstract in Portuguese is available at http://www.blackwell-synergy.com/loi/btp

Key words: aboveground tree live biomass; allometric equations; permanent plots; rate of change; soil texture; temporal variation; *terra firme* forest; topography; tree size distribution.

LIVING TREES CONSTITUTE one of the largest carbon stocks in tropical forests, which, in total, store nearly 40 percent of all the carbon residing in terrestrial vegetation worldwide. This means that tropical forests play a fundamental role in the carbon cycle, influencing the current atmospheric concentration of CO_2 as both a source, following land-use and land-cover changes, and sink, probably resulting from CO_2 stimulation of forest photosynthesis, of carbon (Malhi & Grace 2000). Therefore, determining the current carbon balance of these ecosystems, and reaching a better understanding of how this balance is likely to change, represents an urgent research need for projecting the rate of atmospheric CO_2 accumulation, and its consequences for climate change (Clark 2004).

Permanent tropical forest plots offer great potential for direct monitoring of aboveground carbon stocks. The ratio of carbon in living tissues is, in general, half of the plant biomass (Malhi & Grace 2000); therefore, carbon uptake can be detected through evidence of tree biomass increase. Biomass estimates can be easily obtained from allometric equations based primarily on tree diameter. This approach has been used in the past few decades to determine trends and rates of aboveground tree live biomass (AGLB) in permanent plots spread over the Amazon (*e.g.*, Phillips & Gentry 1994, Phillips *et al.* 1998, Baker *et al.* 2004). Although widely spaced plots measured over a variety of time intervals are extremely useful for evaluating the generality of trends (*e.g.*, Baker *et al.* 2004), they have limitations for investigating possible mechanisms. Also, overall biomass change may mask changes in different size classes of trees. To separate climatic and other geographic factors from soil and topographic effects, it is necessary to have a large number of replicates within a limited geographic region. Because relationships may change through time, it is also necessary to have replicate samples in the same region in different time periods to evaluate the consistency of trends.

Because of its continental scale, Amazonian rain forests occur in different climatic regimes, topography and consequently forest structure and biomass. Currently, the amount and spatial distribution of forest biomass in the Amazon basin is a major source of uncertainty in estimating the carbon balance (Saatchi *et al.* 2007). Besides this, spatial components of temporal variation of biomass are poorly documented in tropical forests. In central Amazonian forests, AGLB exhibits great spatial variation in a scale of ten to hundreds of kilometers (Laurance *et al.* 1999, Castilho *et al.* 2006), but how this variation is maintained, or whether it changes through time, is largely unknown.

In a previous study, we showed the predictive power of soil and topography based on models of AGLB spatial variation over 64 km^2 of old growth *terra firme* forest. In our study area, the soil textural gradient varies from 1.6 to 87.7 percent of clay, even though the altitudinal variation is generally < 70 m (see Castilho *et al.* 2006 for details). Clay soils generally show greater AGLB than sandy soils. This difference could be due to different plant composition among soil types or differences in growth and mortality rates among soil types, even without differences in plant composition. Both explanations can result in spatial distribution of AGLB that could be maintained through time. Here, we add the temporal component to our estimates, analyzing how AGLB changes through time and how time could affect the spatial variation previously found.

In this study, we present the results of the monitoring of permanent plots over a 2-yr interval, to assess the short-term trend and

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rate of AGLB change in a soil and topographic gradient typical of central Amazonia. The plots were measured between December 2000 and February 2005. We addressed the following questions: (1) what is the trend and rate of change in AGLB in this forest? (2) Is the rate of change similar for different tree size classes? (3) Is soil (texture and nutrients) or topography (elevation and slope) related to temporal variation in AGLB in this forest? (4) If soil or topography is related to the rate of AGLB change, is this relationship constant through time?

It is challenging to accurately measure AGLB change using short-term intervals (*i.e.*, 2 yr) because measuring small changes in diameter is more error prone than measuring large changes. However, long census intervals may not detect changes associated with short-lived species (Sheil & May 1996), and variation in weather relevant to trees may occur at shorter intervals. El Niño events occur at intervals of 3–5 yr (Marengo 2004), and studies with growth bands indicate that trees may respond to weather conditions at a scale of days (Clark *et al.* 1999). By using a large number of plots, we were able to detect effects that would be below the level of precision of individual plots, and there was no relationship between the effects detected and the small variation in census interval. However, our conclusions apply only to the intervals studied, and ongoing long-term studies will determine whether these trends are maintained.

METHODS

Background.—There are two basic approaches to estimating AGLB over large areas: one is to randomly or systematically survey an area with a large number of plots, and the other is sampling fewer but larger plots. Under the first approach, the optimal plot shape would be circular, or some other shape with a small perimeter to area ratio, and the size of the plot should be as small as feasible to increase the number of plots that can be sampled (*e.g.*, Clark & Clark 2000). The problem with very small plots is that the overall perimeter to area ratio of all plots is large and it would be very expensive to access plots in remote areas. An alternative is to use larger plots, but this reduces the number of plots that can be used to sample the landscape. Keller *et al.* (2001) recommended that at least 25 0.25 ha plots be used to estimate AGLB for a given forest type. Because there is large variation in rates of AGLB loss and accumulation at small scales, and instantaneous rates of change can be much larger for loss than for accumulation, estimates of biomass change will be positively biased if based on a small number of plots, even if those plots are relatively large (Fisher *et al.* 2008).

Although widely spaced plots are extremely useful for evaluating general trends, they have limitations for investigating possible mechanisms. While this sampling strategy may be appropriate if forests are relatively homogeneous, mean values may not be useful for management if different processes are occurring at different sites. With this in mind, we adopted a sampling strategy named RAPELD, which stands for rapid assessments and long-term ecological research (Magnusson *et al.* 2005), designed to obtain data to model responses in relation to processes known or expected to affect biomass accumulation and change. This system was created to allow the development of precise models of biodiversity variation in relation to the principal edaphic, topographic and hydrological variables thought to most influence ecological processes at meso-scales (tens to hundreds of kilometers) (Magnusson *et al.* 2005). To make available data for modeling, the RAPELD system was designed to provide accurate measurements of predictor and dependent variables.

Study site.—The study was conducted at Reserva Ducke, a 10,000 ha (10 × 10 km) reserve located 26 km north-east of Manaus, Amazonas, Brazil (02°55′ S, 59°59 W). The reserve is in the process of becoming isolated from other forested areas. Although the predominant winds are from the north-east, and blow from the reserve toward Manaus, local climatic effects and nitrogen deposition due to the proximity of the city are likely to affect ecological processes in the reserve in the long term.

Reserva Ducke is one of the most intensively studied sites in the Neotropics. A number of field guides based largely on the reserve (Ribeiro *et al.* 1999, Adis 2001, Lima *et al.* 2006, Vitt *et al.* 2008) make ecological research much easier than in most Amazonian localities, and a network of trails makes most of the 100 km^2 of the reserve readily accessible.

The vegetation of the reserve is classified as *terra firme* forest with closed canopy, and its understory is characterized by abundant acaulescent palms (Ribeiro *et al.* 1999). Canopy height is generally 30–37 m, with individuals that reach 40–45 m. Average annual rainfall at this site is about 2300 mm, with a distinct dry season between July and September, and usually 3 mo with > 100 mm of rain (Marques-Filho *et al.* 1981). Mean monthly temperature is stable throughout the year, varying little around 26°C (Marques-Filho *et al.* 1981).

The reserve is covered mostly by Oxisols (allic yellow latosols in the Brazilian system) on the plateaus, Ultisols (podzol in the Brazilian system) on slopes and Spodosols associated with small streams in valley bottoms (Chauvel *et al.* 1987, Bravard & Righi 1989). These soils are typically acidic and very low in nutrients, such as phosphorus, calcium and potassium (Chauvel *et al.* 1987). The topography of the reserve is undulating with a dense drainage network forming a pattern of plateaus and valleys with a maximum height difference of about 100 m (40–140 m asl; Ribeiro *et al.* 1999). When moving from a plateau to a valley, clay content decreases strongly and sand content increases (Chauvel *et al.* 1987).

Sampling design.—We systematically distributed 72 1-ha permanent plots over an area of 64 km^2 to encompass the main gradients in soil and topography found at Reserva Ducke. All plots were at least 1 km from the edge of the reserve and from one another. More detailed information about the sampling design can be found in Magnusson *et al.* (2005) and Castilho *et al.* (2006).

Each permanent plot is 250 m long and the center line follows an altitudinal contour. The advantage of this design is that narrow plots following contour lines tend to keep soil conditions homogeneous, given that soil types vary with altitude in central Amazonia (Chauvel *et al.* 1987). Long thin plots that follow the altitudinal contours have negligible variation in altitude, and generally have little variation in soil characteristics and distance to the water table in relation to square plots. In the Manaus region, a randomly placed

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square 1-ha plot could have a corner in sandy hydromorphic soil, and another corner in clay soil 20 m above the water table. Representing the conditions in such plot as 50 percent sandy soil and 10 m above the water table would not allow precise modeling. The disadvantage is that long thin plots have a higher perimeter to area ratio than circular or square plots, and this could reduce precision of density estimates if many individuals at the edges of plots are falsely included or excluded. However, even if some individuals are wrongly included or excluded, this will not bias results as long as the probability of a wrong exclusion is the same as a wrong inclusion. For modeling biomass change within a RAPELD grid, the objective is to obtain relationships averaged over all the plots (72 in the case of Reserva Ducke) and not to obtain extremely precise estimates for individual plots. A possible loss of precision in biomass estimates because of the use of long thin plots is more than offset by the precision of the predictor variables when modeling is the objective.

The 250-m-long plots have a width of 40 m, resulting in a 1 ha total area, where all trees with dbh $\geq$ 30 cm were sampled. Subsamples of 0.5 ha (20 $\times$ 250 m) and 0.1 ha (4 $\times$ 250 m) were used to sample trees with 10 cm $\leq$ dbh $<$ 30 cm and 1 cm $\leq$ dbh $<$ 10 cm, respectively.

All plots had the same horizontal area, independent of their topography. Otherwise plots that have 1 ha on the ground will have $<$ 1 ha available for treecrowns (planar area) in steep areas. The limits of the plots were established using a tape horizontally placed over the terrain between the central line and the edge of the plot. An advantage of using planar area is that it facilitates the transfer of the limits of the plot to maps or satellite imagery. All results are qualitatively similar for data analyzed per hectare of ground area (Castilho 2004).

CENSUS TECHNIQUES.—Within our plots, all trees were marked with aluminum numbered tags, mapped, and their diameters were obtained by carefully measuring (to the nearest mm) the diameters of all trees $\geq$ 1 cm at breast height (dbh = 1.3 m aboveground). Protocols for diameter measurements depended on tree size. For individuals $<$ 6 cm diam, maximum stem diameter was measured with calipers. Boles $>$ 6 cm diam were measured with a fabric diameter tape (Forestry Suppliers, model 283D, Jackson, MS, U.S.A.). When the point of measurement (POM) was affected by buttresses or major stem deformities, measurements were taken 50 cm above the deformity. We used ladders to measure boles above buttresses and other irregularities. The measures were done at permanently marked points. All changes in POM in subsequent censuses were documented. In case of changing POM, we made one measurement at the original POM and another at the new point to permit comparisons between censuses. Hereafter, stem diameter is abbreviated dbh whether it was precisely at breast height or not.

Before running the analyses we checked the entire data base for obvious typographical errors or unusual measurement values. We found problematic tree records that included: (1) small discrepancies in remeasurement of the same stem; or (2) large discrepancies resulting from measurement errors or change in the POM. Small discrepancies were generally ignored, because our large samples should produce overestimates as often as underestimates, and should not bias estimates of the mean (Condit *et al.* 2004). Large discrepancies were corrected on a tree-by-tree basis either by excluding the individual or assuming zero growth. We used this approach for cases where the change of POM prevented a proper comparison of dbh change between censuses.

BIOMASS ESTIMATES.—We converted dbh measurements of each tree to an aboveground dry biomass estimate with a combination of general allometric models developed from local forests, depending on tree diameter class (Table S1). AGLB estimates for trees with dbh $<$ 30 cm were extrapolated to 1 ha, based on our subsample estimates.

Biomass addition arises partly from growth of the subset of trees that were alive in both censuses, which was calculated as the difference in biomass between 2001/2003 and 2003/2005. Trees growing into the smallest size class (dbh $\geq$ 1 cm) were added to the sample as recruitment. Trees that had not previously been measured were also recruited into the larger size classes (dbh $\geq$ 10 cm or $\geq$ 30 cm) because plots for each size class have different dimensions. We are aware that by including trees $>$ 30 cm as recruits, we are adding the growth of the tree's entire life to an annual measurement. To account for this bias we also estimated the rate of AGLB change excluding these individuals (data not shown), and general trends remained similar. Biomass additions due to recruitment were determined with the same allometric equations. To analyze the changes of AGLB on each size class, we considered all transitions within the nested series of plots as growth, and all growth to the set of minimum diameters from areas outside the plots as recruitment. Trees with no foliage and dry sapwood all around the trunk were recorded as dead. The biomass for each tree that died was determined using the same allometric equations applied to live biomass, employing the last measured dbh before death.

CENSUS INTERVAL.—The first census was undertaken between December 2000 and February 2003. Resurvey of all tagged stems was done between February 2003 and February 2005. The mean interval between censuses was 2 yr (SD = 7 d; Table S2). One plot was resurveyed after 26.5 mo. To avoid the effect of different intervals between censuses, we ran all analyses with and without that plot. Thirty plots were surveyed between January 2001 and December 2003. Another 35 plots were surveyed between January 2002 and December 2004. Six plots were surveyed between January 2003 and February 2005. Plots surveyed in each interval were distributed throughout the reserve to avoid confounding temporal and spatial effects.

Measurements in the first census were supervised by the same person (R. N. O. de Araújo) and four different people measured dbh. All re-census dbh measurements were done by the same field assistant (J. B. Souza), supervised by R. N. O. de Araújo.

SOIL AND TOPOGRAPHIC DATA.—To represent soil properties in each plot, we used a composite sample consisting of six topsoil (0–5 cm deep) cores taken every 50 m along the 250 m centerline of each plot. Composite samples for each plot were oven-dried and cleaned by removing stones and fine roots before being used to determine

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texture (percent of clay and silt); pH in water; and amount of primary nutrients (P and K^+), secondary nutrients (Ca^{2+}, Mg^2 and Na^+), micronutrients (Cu^+, Fe^{2+}, $Mn^{2+}$and Zn^{2+}) and other ions (Al^{3+} and $Al^{3+}+H^+$). Detailed information about field and laboratory methods used for soil analyses were presented by Mertens (2004) and summarized in Castilho *et al.* (2006). All soil analyses were conducted at National Institute for Research in the Amazon or Brazilian Agricultural Research Corporation laboratories.

The topographic variables used in this study were elevation and slope. A professional surveyor determined the elevation at the beginning of the plot. The slope across the plot was measured with a clinometer, every 50 m along the 250 m centerline of each plot, totaling five measurements per plot. The slope angle was measured over a distance of 5 m (2.5 m each side of centerline), perpendicularly to the altitudinal contour lines. We used a mean of the five measurements to represent the slope of the plot.

SOIL GRADIENTS.—We used principal components analysis (PCA) to describe major gradients in the soil using a subset of 14 variables (see Castilho *et al.* 2006 for details). The ordination analysis revealed three main soil gradients in the study area. Axis 1, which captured 34 percent of the total variation in the dataset, described a textural gradient between plots with high clay content (also high K^+, Mg^{2+}, Na^+, Al^{3+} and $Al^{3+}+H^+$), and those with high sand content. Axis 2, which explained 23 percent of the variation, mainly described a continuum in soil pH, with more acidic sites having higher Fe^{2+} and Al^{3+}, and less P, K^+, Ca^{2+}, Mg^{2+}, Mn^{2+} and Zn^{2+}. Axis 3 explained 8 percent of the variation and described a gradient between sites with low percentages of silt and P and sites with high values for these variables.

RATE OF AGLB CHANGE.—The rate of AGLB change is the difference between AGLB in the second census and AGLB in the first census. The AGLB in the second census is the result of tree growth plus recruitment, minus tree mortality. Results are expressed as the crude rate (AGLB2 − AGLB1). To deal with the skewed distribution of the rate of AGLB change among our plots (right tail slightly longer than expected under a normal distribution) we also calculated confidence limits using a bootstrapping technique (1000 replicates) to check the accuracy of the parametric confidence limits. Statistically significant differences between estimates were assumed when 95% confidence limits did not overlap (Condit *et al.* 2004).

EFFECTS OF SOIL AND TOPOGRAPHY ON THE RATE OF AGLB CHANGE.—To test the joint effects of soil gradients and topography on AGLB temporal variation, we used multiple regression analyses. Pearson's correlations were used to test for collinearity between soil gradients (PCA axes) and topography. As elevation and the first PCA axis were highly correlated ($r = 0.76$), we did not include them in the same analyses. First, we tested the relationships between slope and the three PCA axes with rate of change in AGLB over the time interval. We then tested for a relationship between the topographic variables (elevation and slope) and the rate of AGLB change. We used SYSTAT 8.0 statistical package for all analyses (Wilkinson 1990). To test for spatial autocorrelation on the rate of AGLB change per plot, we used the Moran's I (Moran 1950) as a measure of the degree of dependency among observations in space and 1000 permutations to calculate the probabilities associated with the null hypothesis for each distance class in the Spatial Analysis in Macroecology Program (Rangel *et al.* 2006).

ERRORS ASSOCIATED WITH AGLB ESTIMATES.—We chose the best available model for our region, which was developed *ca* 60 km from our study site from a sample of 315 trees with dbh of 5–120 cm (Higuchi *et al.* 1998). Because we used the same model to estimate AGLB for all 72 plots, any possible errors associated with the models should be equal for all plots. One problem with the use of this model is that it provides fresh-weight estimates of AGLB. According to Higuchi *et al.* (1998) the dry-weight is around 60 percent of the tree fresh-weight; therefore we used a standard value of 0.60 to convert the estimates into dry-weight. The downside of this approach is that the water content in living tissues may vary among size class, species and sites, but at present we lack general values to assess this possible variation. In our case, it should not strongly bias our conclusions because we are comparing AGLB estimates within a single region in central Amazonia. We do not recommend using the same value if the data would be compared between different regions (see Nogueira *et al.* 2008).

All results presented in the manuscript were based on AGLB estimates obtained using Higuchi's model. To see whether the results were affected by our choice of the allometric model we also report AGLB estimates using: (1) an equation that directly calculates dry-weight biomass (Chambers *et al.* 2001); and (2) two models that include wood-density data for trees with dbh $\geq$ 10 cm (Chambers *et al.* 2001 modified by Baker *et al.* 2004 and Chave *et al.* 2005; Table S3). Wood-density data were obtained from Chave *et al.* (2006) based on floristic data from our plots. In the absence of species-level information, we used genus or family-level wood density means, as suggested by Chave *et al.* (2006). The comparisons among models were done excluding trees $<$ 10 cm in dbh, which are beyond the range of some equations.

Another possible source of error is dbh measurements. Although we did not perform a double-blind remeasurement of some trees to estimate rates of measurement errors (as desired), we are assuming that possible errors associated with the measurements are equally distributed in all plots, because the same person remeasured all trees in the studied plots. We believe that the errors associated with AGLB estimates do not compromise our results because they are based on a comparative approach of 72 1-ha plots carefully established and measured to avoid sources of variability other than the factors studied.

RESULTS

RATE OF AGLB CHANGE.—The mean AGLB at Reserva Ducke increased significantly from 321 to 324 Mg/ha over a 2-yr interval (paired *t*-test: $t = -4.84$, df = 71, $P < 0.001$). Over that interval, the mean rate of AGLB change was 1.65 Mg/ha/yr (bootstrapped 95% CI: 1.15, 2.79), ranging from − 13.25 to 13.11 Mg/ha in 2 yr (Table S2). Most plots had a net increase in AGLB (Fig. 1). The

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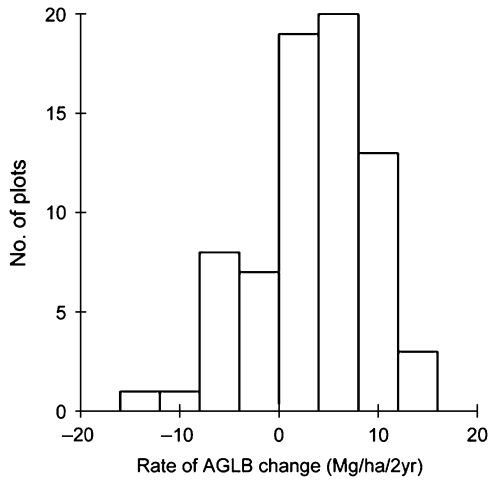

FIGURE 1. Frequency distribution of the rate of aboveground tree live biomass (AGLB) change in seventy-two 1 ha permanent plots at Reserva Ducke, over an interval of 2 yr (2001–2003/2003–2005).

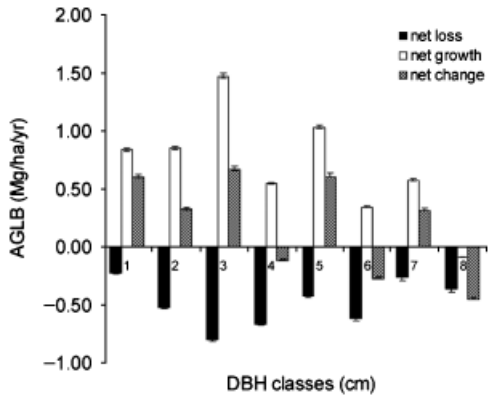

FIGURE 2. Changes in aboveground tree live biomass (AGLB) by diameter class (cm), over 1 yr in 72 ha of *terra firme* forest in central Amazonia. 1 = 1 ≤ dbh < 10; 2 = 10 ≤ dbh < 20; 3 = 20 ≤ dbh < 30; 4 = 30 ≤ dbh < 40; 5 = 40 ≤ dbh < 50; 6 = 50 ≤ dbh < 60; 7 = 60 ≤ dbh < 70; 8 = dbh ≥ 70 cm. To calculate the changes we considered all transitions within the nested series of plots as growth and all growth to the set of minimum diameters from areas outside the plots as recruitment. Error bars are 95% CIs of the mean values.

mean rate of AGLB increase (growth + recruitment) was 5.6 Mg/ha/yr (95% CI ± 0.89 Mg/ha/yr), and the mean rate of AGLB loss was 3.9 Mg/ha/yr (95% CI ± 0.63 Mg/ha/yr; Table S2).

There was no significant spatial autocorrelation in AGLB rate of change at any distance ($P < 0.001$), and the highest value of Moran's I was only 0.08. There was also no significant spatial autocorrelation in the residuals from the multiple regression at any distance ($P < 0.001$, Moran's I max. = 0.09).

RATE OF AGLB CHANGE IN RELATION TO TREE SIZE.—The rate of AGLB change differed among tree size classes. Over an interval of 2 yr, most (43%) of the AGLB gained was in the dbh < 30 cm classes and as much as 26 percent was in the 20–30 cm class, which represents mainly subcanopy trees (Fig. 2). AGLB loss was concentrated in trees with < 40 cm dbh (Fig. 2). AGLB change was negative only for tress with 30–40, 50–60 and ≥ 70 cm dbh.

The rate of AGLB change was significantly positive for trees with dbh < 30 cm and for trees with 40 ≤ dbh < 50 cm (Table S4). Most canopy, subcanopy and emergent trees did not experience significant changes in AGLB between censuses (Table S3).

EFFECTS OF SOIL, TOPOGRAPHY AND PERIOD OF MEASUREMENT ON THE RATE OF AGLB CHANGE.—Multiple regression analysis using data from the whole survey period (N = 72 plots) indicated that the rate of AGLB change was not related to any of the PCA axes or to slope ($F_{4,67}$ = 0.52, P = 0.72). The regression using only topographic variables (altitude and slope) also did not explain temporal variation in AGLB ($F_{2,69}$ = 0.13, P = 0.88). However, plots monitored in 2001–2003 (N = 30) showed different relationships to independent variables than plots (N = 35) monitored in 2002–2004 (Fig. 3). The mean yearly rate of change in AGLB for these plots was 1.14 (95% CI ± 1.25 Mg/ha/yr).

There was a statistically significant interaction between the soil textural gradient (PCA axis 1) and the period in which the plots were monitored (ANCOVA: $F_{1,68}$ = 5.3, P = 0.024). For plots monitored between 2001 and 2003, the soil textural gradient explained 17 percent of the AGLB change ($F_{1,28}$ = 5.84, P = 0.02). Positive rates of change occurred in clay-rich soils while sandy soils had a tendency to lose biomass over the same period. No relationship between soil and AGLB accumulation was apparent for plots monitored in the 2002–2004 interval ($F_{1,33}$ = 0.78, P = 0.38). The mean yearly rate of change in AGLB for these plots was 2.29 (95% CI ± 0.84 Mg/ha/yr). Although there was no linear trend in the second census interval, the variance in biomass change on sandy soils (29.9; those on Fig. 3 with PCA score < 0) was significantly greater than on clay soils (21.7; Bartlett's test: B_c = 4.63, $P < 0.05$).

EFFECTS OF ALLOMETRIC MODEL ON AGLB RATE OF CHANGE.—We made two different comparisons to assess the effects of the allometric models on our results. We first compared the results, obtained using the equation provided by Higuchi *et al.* (1998) and by Chambers *et al.* (2001), which directly calculates dry-weight biomass. The mean rate of AGLB change using Chamber's equations (1.61 Mg/ha/yr; 95% CI ± 0.70) was not significantly different from Higuchi's model, although AGLB estimates were around 10 percent higher (data not shown). We then used preliminary floristic data to apply equations that use wood density. This comparison could only be done with trees with dbh ≥ 10 cm, because trees with dbh < 10 cm are beyond the range of some equations. Equations that include wood density showed lower mean rates of AGLB change (Chave's model: 0.64 Mg/ha/yr; 95% CI ± 0.92 and Chambers *et al.* with wood-density model: 0.71 Mg/ha/yr; 95% CI ± 0.78) than Higuchi's model (1.05 Mg/ha/yr; 95% CI ± 0.71). These rates, however, were not significantly different among them (Kruskal–Wallis test statistic = 0.203, P = 0.93; Fig. S1). Although wood-density models estimated lower rates of AGLB change, they provided AGLB estimates that were also 10 percent

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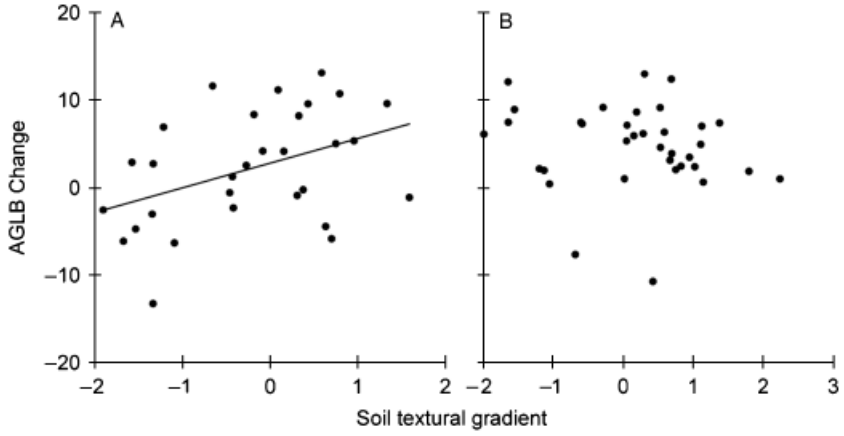

FIGURE 3. Relationship between aboveground tree live biomass (AGLB) changes (Mg/ha/2 yr) and soil textural gradient (PCA axis 1) in different time intervals. Positive values in the soil textural gradient represent plots with clay soil. (A) Rate of AGLB change was related to the soil textural gradient for trees in plots measured between 2001 and 2003. Plots on sandy soil tended to loose biomass, while biomass increased on clay soils. (B) Rate of AGLB change was not related to soil textural gradient for trees in plots measured between 2002 and 2004. PCA, principal components analysis.

higher than models that do not incorporate wood density. AGLB estimates using Higuchi's model were correlated with estimates using Chave's model ($r = 0.98$) or Chamber's modified model ($r = 0.95$).

The trend of biomass increase over the 2-yr interval was statistically significant throughout the different models, except for Chave's model. The relationship between rate of AGLB change, soil and time interval was not affected by the allometric model used, suggesting a consistent trend (Table S5).

DISCUSSION

This study demonstrates that, during a 2-yr interval, AGLB increased by 3.3 Mg/ha (1.67 ± 2.9 Mg/ha/yr) in a forest near Manaus. This value is greater than the mean value of AGLB change reported by Baker *et al.* (2004) for 25 plots monitored in sites located in central and eastern Amazonia whose results showed that AGLB of trees > 10 cm dbh increased by 0.73 ± 0.68 Mg/ha/yr.

Some studies have related biomass change to an increase in tree turnover in Amazonian forests over the last decades (Phillips & Gentry 1994, Lewis *et al.* 2004, Phillips *et al.* 2004), suggesting that forests are becoming denser due to an increase in recruitment rates. At Reserva Ducke, during a relatively short period of time, biomass increase was mainly the result of tree growth, and not recruitment.

AGLB changes exhibited large variability, ranging from − 13.25 to 13.11 Mg/ha over 2 yr. Some of the variability between plots seems to be caused by variability in the natural disturbance regime. Some of the plots with higher rates of AGLB increase may be recovering from mortality events before plot establishment, while negative rates may indicate that the plots had experienced a disturbance during the monitored interval. The years previous to our plot establishment were marked by a strong El Niño event (1997–1998) followed by a La Niña event (1999–2001) (http://enos.cptec.inpe.br); both events elevate tree mortality in Neotropical forests (Williamson *et al.* 2000). When trees fall, a canopy gap is created, stimulating recruitment of new trees, high levels of leaf production and tree growth, which can cause net accumulation of live biomass. At Reserva Ducke, AGLB losses varied from 0.5 to 8.3 percent of the original biomass of the plot. Most plots (55%) lost < 2 percent of their original biomass over a 2-yr interval. Because losses occur more quickly than recovery, individual plots are more likely to record growth than losses (Fisher *et al.* 2008). Even though our analyses are based on a large number of plots, large losses of AGLB (> 8 Mg/ha/yr) were rare in our sample (only 7% of the plots) and were not related to either soil or topography.

Another source of variability in AGLB change is plot species composition. Patterns of tree growth, longevity and mortality are species-specific (Korning & Balslev 1994, Clark & Clark 1999, Laurance *et al.* 2004a) and these traits may be driving the rate of change in each plot. Moreover, some population trends are unpredictable and interact with site factors. Some species may perform poorly at one site and decline in abundance, while other populations may be stable or increase in abundance at other sites (Condit *et al.* 2004).

Despite the fact that some studies have shown that soil explains around one-third of the spatial variation of AGLB in central Amazonia (Laurance *et al.* 1999, Castilho *et al.* 2006), the short-term rate of AGLB change seems to be unpredictable based on soil or topographic data alone. Long-term studies suggest that soil quality could affect tree recruitment and mortality in tropical forests (Phillips *et al.* 2004) and consequently they could affect the rates of AGLB change. The short-term rate of change could be determined by stochastic processes, such as large tree mortality, representing the loss of a large amount of plot biomass followed by a biomass increase as other trees are favored by the gap created.

The rate of change in AGLB for plots measured in 2001–2003 (1.14 ± 3.3 Mg/ha/yr) was similar to that for plots measured in 2002–2004 (2.3 ± 2.4 Mg/ha/yr) ($t = -1.63$, df = 63, $P = 0.11$). However, different processes may have been acting during these two time intervals. Rate of change in AGLB was associated with soil

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characteristics in the first period, but not in the second. This is unlikely to be an effect of sampling because the relationship was based on a large number of plots (30) in the first interval, and even more (35) in the second. In any case, the variance in biomass change on sandy soils remained higher than the variance in biomass change on clay soils. As much of Amazonia has low-lying sandy soils similar to those at Reserva Ducke, models of biomass change should take into account potential differences in processes associated with edaphic features. Our data are too limited to warrant speculation on the reasons for these differences among soils in different periods, but they do indicate that temporal and spatial factors may interact, and that care must be taken in the interpretation of relationships identified in any one census interval.

Rates of AGLB change at Reserva Ducke are dependent on tree size. This was expected because the pattern of growth in diameter is highly dependent on tree size (Clark & Clark 1999). In general, most canopy and emergent trees did not experience significant changes in AGLB. Accumulation of live biomass was concentrated in the smaller classes (understory and subcanopy trees) (Chave *et al*. 2003, Rice *et al*. 2004, this study), suggesting that the site is recovering from a significant disturbance in years preceding this study. We also recorded a significant AGLB increase in trees with $40 \leq \text{dbh} < 50$ cm. Trees of this size occupy the canopy and have a greater energy supply and higher photosynthetic rates (Hubbell *et al*. 1999) and are therefore more prone to grow and accumulate biomass. However, emergent trees had a negative net change in AGLB that could be the result of biological limitations on tree size or a response to recent climatic conditions. Clark and Clark (1996) suggested that large trees (> 70 cm dbh) are more drought susceptible than smaller trees. The negative AGLB net change of large trees was explained by the negative growth rates and by the fact that around 10 percent of total AGLB loss was due to large tree mortality over the studied time interval. Negative growth rates could result from error measurements. According to an allometric rule, a millimeter of diameter in a large tree represents a manyfold higher biomass accumulation (or loss) than a millimeter of diameter change in a small tree. This point reinforces the necessity of paying close attention when estimating growth rates of large trees. It is likely that a larger measurement interval may be more appropriate to detect the 'real' growth within measurement error. Another option could involve taking replicate measurements along the stem of each tree to better estimate the biomass accumulation of large trees.

In recent years several authors have highlighted the necessity of reporting errors associated with biomass estimates. The current consensus is that one of the most important sources of error is related to the choice of the allometric model (*e.g*., Chave *et al*. 2004). Our results showed that the rates of AGLB change at Reserva Ducke were sensitive to the equation used to estimate tree biomass. Although allometric models introduce uncertainty in the magnitude of the change, the trend (biomass increase) remained consistent among all models. This increase was significantly positive across different equations, except in Chave *et al*. (2005) model. Overall, allometric models that include wood density resulted in lower AGLB rates of change, even considering that these models estimated higher AGLB per plot. These differences could suggest that the growth and/or recruitment in our plots have been concentrated in low-wood-density species or that biomass loss was represented by high-wood-density species. Pervasive alterations in tree community composition favoring fast-growing species over slow-growing ones have been suggested to occur in undisturbed Amazonian forests (Laurance *et al*. 2004b). This issue deserves further investigation and indicates that potential changes in tree composition may also have important implications for carbon cycling and biodiversity, as changes in forest biomass are coupled to changes in species composition.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Allometric equations used to estimate tree aboveground dry biomass based on dbh*.

TABLE S2. *Rate of aboveground live biomass change over an interval of two years in 72 1-ha permanents plots located at Reserva Ducke (Manaus, Amazonas)*.

TABLE S3. *Rate of aboveground live biomass (AGLB) change in 72 1-ha permanent plots located at Reserva Ducke (Manaus, Amazonas) estimated using different allometric models*.

TABLE S4. *Results of a paired* t*-test comparing mean AGLB per diameter class over an interval of two years*.

TABLE S5. *Results of simple regressions relating the rate of AGLB change using different allometric models with a soil textural gradient for plots monitored between 2001–2003*.

FIGURE S1. Estimates of AGLB change per plot for trees with dbh ≥ 10 cm, based on three different allometric equations.

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