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Forest structure and carbon dynamics in Amazonian tropical rain forests

Abstract Living trees constitute one of the major stocks of carbon in tropical forests. A better understanding of variations in the dynamics and structure of tropical forests is necessary for predicting the potential for these ecosystems to lose or store carbon, and for understanding how they recover from disturbance. Amazonian tropical forests occur over a vast area that encompasses differences in topography, climate, and geologic substrate. We observed large differences in forest structure, biomass, and tree growth rates in permanent plots situated in the eastern (near Santarém, Pará), central (near Manaus, Amazonas) and southwestern (near Rio Branco, Acre) Amazon, which differed in dry season length, as well as other factors. Forests at the two sites experiencing longer dry seasons, near Rio Branco and Santarém, had lower stem frequencies (460 and 466 ha^{-1} respectively), less biodiversity (Shannon–Wiener diversity index), and smaller aboveground C stocks (140.6 and 122.1 Mg C ha^{-1}) than the Manaus site (626 trees ha^{-1}, 180.1 Mg C ha^{-1}), which had less seasonal variation in rainfall. The forests experiencing longer dry seasons also stored a greater proportion of the total biomass in trees with >50 cm diameter (41–45 vs 30% in Manaus). Rates of annual addition of C to living trees calculated from monthly dendrometer band measurements were 1.9 (Manaus), 2.8 (Santarém), and 2.6 (Rio Branco) Mg C ha^{-1} year^{-1}. At all sites, trees in the 10–30 cm diameter class accounted for the highest proportion of annual growth (38, 55 and 56% in Manaus, Rio Branco and Santarém, respectively). Growth showed marked seasonality, with largest stem diameter increment in the wet season and smallest in the dry season, though this may be confounded by seasonal variation in wood water content. Year-to-year variations in C allocated to stem growth ranged from nearly zero in Rio Branco, to 0.8 Mg C ha^{-1} year^{-1} in Manaus (40% of annual mean) and 0.9 Mg C ha^{-1} year^{-1} (33% of annual mean) in Santarém, though this variability showed no significant relation with precipitation among years. Initial estimates of the C balance of live wood including recruitment and mortality as well as growth suggests that live wood biomass is at near steady-state in Manaus, but accumulating at about 1.5 Mg C ha^{-1} at the other two sites. The causes of C imbalance in living wood pools in Santarém and Rio Branco sites are unknown, but may be related to previous disturbance at these sites. Based on size distribution and growth rate differences in the three sites, we predict that trees in the Manaus forest have greater mean age (~240 years) than those of the other two forests (~140 years).

Keywords Carbon · Forest dynamics · Tropical forest · Growth rate · Dendrometry

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Introduction

Tropical rainforests play an important role in the global terrestrial carbon cycle (Dixon et al. 1994), accounting for

32 (Field et al. 1998) to 36% of terrestrial net primary production (NPP) (Melillo et al. 1993; Potter et al. 1993). The Amazon rain forest, including dense and open forests types encompasses approximately 40% of the total tropical forest areas of the Earth (FRA FAO 2001), approximately 365 million hectares (Braga 1979), and contain ~30% of global vegetation carbon stocks. More than 50% of the carbon in Amazonian rainforest is in the form of woody biomass: tree trunks, branches and large roots (Brown et al. 1995; Keller et al. 2001). A number of studies (Trumbore et al. 1995; Camargo et al. 1999; Bernoux et al. 2002; Telles et al. 2003) have shown that large stocks of C in tropical soils are mostly associated with material that is preserved for centuries and longer. Hence, the dynamics of wood and woody debris will dominate the short-term response of C storage in these forests (Phillips et al. 1998; Chambers et al. 2001a).

At the continental scale, the Amazon basin includes considerable variation in climatic regime, topography, and geography (Elsenbeer and Lack 1997), and carbon cycle dynamics that vary with these factors (Vetter and Botosso 1989; Clark and Clark 1994; Malhi et al. 2002). According to Liebmann and Marengo (2001) the mean precipitation in the Brazilian Amazon varies from less than 2,000 mm year^{-1} in the south, east and extreme north to more than 3,000 mm year^{-1} in the northwest of the region. The dry season in the Amazon basin varies from nonexistent to periods when there are 7 consecutive months with less than 100 mm month^{-1} of rain (Sombroek 2001). A better understanding of aboveground biomass distribution and tree growth across the Amazon basin is of great importance in order to understand how this region's carbon balance responds to climate variability (Schimel 1995; Houghton et al. 2000; Ketterings et al. 2001). The role of the Amazon region in the global balance of carbon, especially the potential of primary forests to act as a source or sink of carbon due to climatic changes depends mainly on the carbon dynamics in trees of *terra-firme* forest Brazilian Amazon (Schimel 1995; Houghton et al. 2000; Ketterings et al. 2001) where 74% of the terrestrial biomass carbon is allocated (Brown et al. 1995). This is a controversial issue since several studies have proposed that the some sites within Amazon forest acts as a sink for carbon (Grace et al. 1995a,b; Malhi et al. 1998; Phillips et al. 1998; Malhi et al. 2002; Phillips et al. 2002), while others may act as a small temporary source of carbon to the atmosphere (Rice et al. 2004; Saleska et al. 2003).

Here, we describe forest structure and growth dynamics of three permanent plots in the Amazon basin. These intensive sites are part of the Brazilian-led LBA (Large-scale Biosphere-Atmosphere Exchange in the Amazon) Project, and include new as well as pre-existing permanent plots. Here, we investigate among these three sites differences in (1) floristic composition, structure and biomass, (2) annual growth increment, and (3) seasonal patterns of growth.

Materials and methods

Study sites

Our three study sites were: (1) the ZF-2 Experimental Station of the Forest Management operated by the National Institute for Research in the Amazon (INPA), located about 90 km North of Manaus, Brazil (60°11′W, 2°58′S); (2) the Catuaba Experimental Farm of Universidade Federal do Acre, (UFAC); located about 23 km from Rio Branco, Brazil (67°62′W, 10°07′S); and (3) the Tapajós National Forest located near Santarém, Brazil (54°95′W, 2°85′S).

Mean annual rainfall in Manaus measured between 1961 and 1990 was 2,285 mm, more than the average annual rainfall of 1,940 mm in Rio Branco (measured from 1969 to 1990) and 1,909 mm in Santarém (measured from 1967 to 1990) (INMET 2001; NuRMA 2002). The major climatic difference among the sites is the seasonality of the distribution of rainfall. Annual movement of the intertropical convergence zone across the Amazon basin results in distinct wet and dry seasons (Marengo and Nobre 2001). Rainfall during dry season months can be quite low (averaging <100 mm month^{-1}) (Sombroek 2001). Roughly 36% of dense *terra-firme* forest in the Amazon basin are located in areas where the precipitation in the driest three months averages <45 mm month^{-1}, and can be as low as <15 mm month^{-1} in the eastern and southern portions of Amazônia (Nepstad et al. 1994). Areas experiencing long dry seasons in eastern Pará are able to maintain broadleaf evergreen forests and high evapotranspiration rates because of water mined by deep-rooting trees (Nepstad et al. 1994). We define the dry season length here as the number of months with rainfall averaging <100 mm month^{-1}. Manaus experiences the shortest dry season (3 months, July–September), Santarém the longest (5 months, July–November), and the dry season in Rio Branco lasts for 4 months (June–September).

Soils at the Manaus and Santarém sites are clay-rich Oxisols with low organic C content, low pH, low effective cation exchange capacity, and high aluminum saturation (Chauvel et al. 1987; Parrota et al. 1995; Ferraz et al. 1998; Telles et al. 2003). Soils at the Catuaba Experimental Farm are classified as dystrophic and eutrophic Ultisols with patchy occurrence of Oxisols (Silveira 2001; Salimon et al. 2004), but at our permanent plot the principal soils are Oxisols, as in the other two areas.

In the Manaus and Santarém sites, the vegetation is dense *terra-firme* (upland) tropical moist forest or "old-growth" (Higuchi et al. 1997; Clark and Clark 1996). The Santarém site is characterized by a larger number of gaps and vines than the Manaus site, while the Rio Branco forest is a mosaic with small patches of dense forest within a large matrix of smaller-stature, open forest with bamboo (Silveira 2001). In Rio Branco, the Catuaba Experimental Farm is an extractive reserve. Although trees have not been logged, there are small trails to support extractive use of trees for rubber and Brazil nut products.

Overall relief varies among the three areas, though we sampled at all sites in upland (*terra-firme*) forest, with slopes of <10%. The major impact related to forest dynamics is likely the accessibility of water for the forests. The Manaus site is dissected by streams that include seasonally flooded areas, with *terra-firme* forest on plateaus roughly 30 m above water table. The Santarém site is located in a large plateau with a deep water table (up to 100 m deep), while at the Rio Branco site the relief is flat with a water table that can come within ~5 m of the surface in the wet season.

Permanent plots

Forest structure, species composition, and growth data were collected in permanent inventory plots established at each of the three sites. In Santarém and Manaus, we took advantage of plots established prior to this study, while in Rio Branco, we established a new permanent plot. As a result, the area and layout of permanent plots differs among the three sites. At all sites, trees >10 cm diameter at breast height (DBH) mapped within each permanent plot

were identified to the genus/species level using field identification. The main diversity indexes were calculated according to Magurran (1988, 2003) and the floristic structure was studied by using Importance Value Index (IVI) (Curtis et al. 1950). DBH was measured at 1.3 m, except for trees with buttresses, where we report diameter measured 10 cm above the buttresses to minimize errors in biomass estimates (Clark 2004).

In Manaus, forest inventory data have been collected since the mid-1980s by the INPA Tropical Forestry group from three plots totaling 3 ha. Within each plot, all stems ≥10 cm DBH were tagged, mapped, and diameters were re-measured annually since the mid-1980s. To study seasonal changes in growth rates, we used monthly dendrometry data from two transect plots (20m ×2,500 m (5 ha) each), established in 1996 by Jacaranda Project (a collaboration between INPA and Japan International Cooperation Agency, JICA). These transects are located several kilometers from the biomass plots and are oriented in east–west and north–south directions so as to include representative spatial samples of upland plateau, slope and lowland areas associated with small streams. The first 2 years of monthly diameter increment data were used to study variation of growth with topography and are reported in da Silva et al. (2002); we include here a third year of measurements. For comparison with the other sites, we have used a subset of data from upland (*terra firme*) sites only (79 trees of a total of 272 bands installed at the Jacaranda plots).

In Santarém, we used data from four plots, totaling 20 ha, established in 1999 by LBA team CD-10 (Dr. Steven Wofsy of Harvard University and Dr. Plínio B. de Camargo of CENA-Nuclear Energy Center of Agriculture; Saleska et al. 2003). These plots consists of transects, each 1,000 m long and 50 m wide. All stems ≥35 cm DBH were included, tagged, mapped and measured. For stems 10–35 cm DBH, four subsets of 4 ha (1,000 m long ×10 m wide) were mapped and measured (Rice et al. 2004).

In Rio Branco, an area totaling 10 ha (200 m ×500 m) was established in 1999 by the SETEM-UFAC group (Sector for Studies of Land Use Change, Federal University of Acre) where all stems ≥35 cm DBH were tagged, mapped and measured. A series of subplots (25 m ×25 m) were established within the 10 ha area, and stems ranging from 10 to 35 cm were tagged in 16 of these subplots (totaling 1 ha).

Within each permanent plot, a subset of the total inventoried stems was selected for dendrometry studies. At Manaus we defined four size classes: small trees (10–29.9 cm DBH), medium trees (30–49.9 cm DBH), large trees (50–100 cm DBH) and giant trees (>100 cm DBH). In Rio Branco and Santarém sites, stems were divided into three size classes (10–35, 35–50 cm and >50 cm DBH) and 100 stems in each size class were randomly selected for installation of homemade stainless steel dendrometer bands (Keeland et al. 1993). Bands were installed in 1998 (Manaus), 1999 (Santarém), and 2000 (Rio Branco), and monitored every 4–8 weeks for growth once an initial several months had passed when the newly installed band adjusts. Our data set represents >300 individuals at Santarém and Rio Branco sites (if trees die, new replacements are randomly assigned), and 79 trees at the Manaus site. Because the size class interval varied among sites, three size classes are reported here: 10–29.9, 30–49.9 and >50 cm DBH. Three years of data (2000–2002) are available from Manaus and 2 (2000–2001) for Santarém and Rio Branco (2001–2002).

Biomass and C inventory

Total aboveground biomass (TAGB) was estimated by applying the allometric equation developed by Chambers et al. (2001b) for the central Amazon:

$$\ln(TAGB) = \begin{aligned} &\alpha + \beta_1 \ln(DBH) \\ &+ \beta_2 [\ln(DBH)]^2 \\ &+ \beta_3 [\ln(DBH)]^3 \end{aligned} \quad (1)$$

where: $\alpha = -0.370$; $\beta_1 = 0.333$; $\beta_2 = 0.933$; and $\beta_3 = -0.122$. This

equation was used to estimate biomass increase from diameter increment at all sites, and carbon inventories were estimated assuming 50% of dry weight biomass is carbon (Brown et al. 1995).

We used the Chambers et al. (2001b) relationship because it is the only one which has been tested outside the area where it was developed. Chambers et al. (2001b) found that an allometric equation based on trees harvested near Manaus gave about the same forest-wide biomass predictions as an allometric equation based on trees harvested in the state of Pará (Araújo et al. 1999). The use of allometry equations outside the regions for which they have been produced is a major source of uncertainty. Allometry equations are based on relating measured tree biomass to factors like tree diameter, or diameter and height, averaged over a large number of individuals (of varying characteristics like wood density). Baker et al. (2004) analyzed data from several sites in Amazonia and found that mean stand-level wood density is greater in the central and eastern Amazon than in northern, or southwest Amazonia. These authors have suggested applying a simple multiplicative density correction factor to the allometry equation to account for these differences (Baker et al. 2004). However, tree height as well as wood density vary among our sites, and may confound the use of this density correction factor. Nelson et al. (submitted) showed that the Chambers et al. (2001a,b), equation overestimates aboveground biomass in the southwestern Amazon by ~22% when both tree height and wood density are taken into account. While acknowledging the inherent uncertainties, we have chosen to report data using the Chambers et al. (2001a,b) for forests in Manaus and Santarém, and to accept the 22% correction suggested by Nelson et al. (2004) for the Rio Branco site, until future tests of the allometry equations are available for these sites. Using the density corrections suggested by Baker et al. (2004) would change our biomass estimates by <1% in Santarém, and result in an 18% reduction of biomass (in contrast to the 22% reduction we have used) in Rio Branco.

Growth rate analysis

Dendrometer bands measure changes in the circumference of the tree; changes in tree diameter were calculated as change in the circumference divided by π. Bands at each of the sites were measured every 4–8 weeks. Due the time interval between measurements varied among sites, diameter variations are reported as monthly means of diameter variation per day (μm day^{-1}). We have made no correction to the data for seasonal variation in stem water content and its potential effect on our measured growth rates; we assume that, averaged over the course of an entire year, the changes in stem water content will be zero. Failure to correct for changes in stem moisture is likely to enhance seasonal contrasts in growth rate.

Estimation of live wood C balance

Biomass increment is an estimate of the wood volume added when diameter increases. The same increase in diameter may give rise to very different increase in biomass for a small tree and a large tree. We calculated biomass increment for each individual using the measured annual diameter increase and the allometric equation of Chambers et al. (2001b); for the Rio Branco site we applied to this the correction factor proposed by Nelson et al. (2004).

Dendrometer measurements yield an estimate of the amount of C allocated to aboveground wood growth in living trees. To accurately estimate the C balance of the living wood pool, adjustments must be made for the amount of C added by recruitment of new trees (in our case, addition of trees that start to exceed 10 cm diameter) and losses by tree mortality. To determine tree recruitment and mortality, permanent plots in Santarém and Manaus are resurveyed annually; the new plot established in Rio Branco was resurveyed after 3 years. We made preliminary estimates of total live wood C balance using the total change over the 3 years between surveys in Rio Branco,

and 2–3 years for which we have dendrometer measurements in Santarém and Manaus. To calculate the carbon budget for the entire live + dead wood pool requires knowledge of the amount and decomposition rate of dead wood in the three areas, which is not yet available.

Results

Floristic composition

Tropical forests are extremely diverse (Simpson index near zero). The three sites we studied varied in dominant tree families and in their degree of diversity as estimated using common indices (Table 1). Our permanent plots contained trees from 52 families at Manaus (3 ha) and Santarém (20 ha), and 40 at Rio Branco (10 ha), totaling 232 species at Manaus, 164 at Rio Branco and 265 at Santarém. The frequency of occurrence of the five most abundant families for each area is shown in Fig. 1.

Expressed on a common area basis, the frequency of species was 163, 127 and 133 species ha^{-1} for Manaus, Rio Branco and Santarém, respectively. The total number of species per unit area identified in our three sites is in accord with values ranging between 90 species ha^{-1} in Rondônia and 285 species ha^{-1} in Manaus given by

Table 1 Summary of floristic attributes of the permanent plots in Manaus, Rio Branco and Santarém

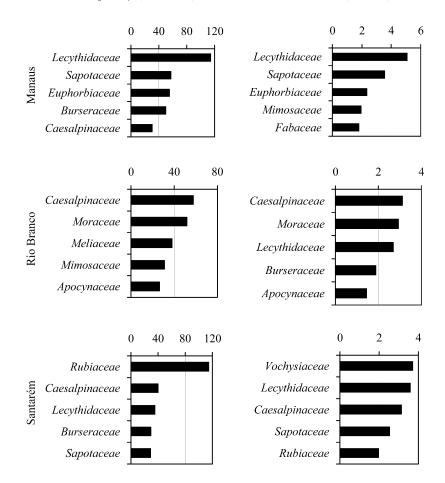| Diversity index	Manaus	Rio Branco	Santarém
Number of individuals per hectare	626	466	460
Number of families in plot area	52	40	52
Number of species in plot area	232	164	265
Number of species per hectare	163	127	133
Shannon–Wiener diversity index	4.67	4.42	4.37
Jentsch coefficient	1/8	1/6	1/9
Simpson index	0.02	0.02	0.04
Pielou index	0.86	0.87	0.78
Jaccard similarity index	0.06[a]	0.05[b]	0.11[c]

[a]Similarity Manaus–Santarém
[b]Similarity Rio Branco–Manaus
[c]Similarity Santarém–Rio Branco

Oliveira and Nelson (2001) for the Amazon region, and indices of diversity generally agree with published values for similar forests (Martins and Santos 1998). All three sites presented high tree species diversity with Shannon index greater than 4 (Table 1). The highest value was found in the forest at Manaus. The Jentsch coefficient value indicates that all three forests are inhomogeneous

Fig. 1 Distribution of the five most frequently observed families in terms of number of individuals per hectare and in terms of the per cent of total basal area (m^2) in the three permanent plots
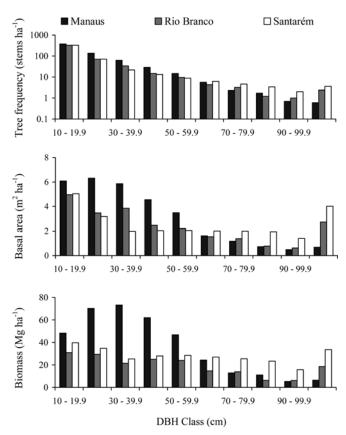
(Table 1), although the values we obtained for the Manaus plot (1:8) is lower than values of 1:14 and 1:12 reported by Higuchi et al. (1998) for a nearby forest. Jardim and Hosokama (1986) reported a value of 1:10 for a separate plot in the Tapajós National forest, similar to our value of 1:9. The distribution of species within a population (according to Pielou Evenness) is more uniform in Manaus and Rio Branco than in Santarém (Table 1). In the JACARANDA project in similar forest in Manaus, Higuchi et al. (1998), reported a Pielou evenness equal to 0.60, compared to our value of 0.86. The three forests represented by our permanent plots are not similar to one another in terms of the species present (Jaccard's index <0.1; Table 1). The greatest similarities are observed for the plots in Rio Branco and Santarém (0.11), which also exhibit similar forest structures.

Structure and biomass

A number of structural and functional differences were found among the sites. Tree density (>10 cm DBH) was greatest in Manaus (626 individuals ha^{-1}), with fewer stems ha^{-1} in the sites with longer dry seasons (466 ind. ha^{-1} in Rio Branco and 460 ind. ha^{-1} in Santarém; Fig. 2a). The three areas differed when distributed among diameter classes. For example, 14.5% of the trees in the central Amazon forest represented by the Manaus site were found in the medium (30–49.9 cm DBH) size class, whereas at the Rio Branco and Santarém sites, only 10.5 and 7.7% of the stems were medium-sized trees. Since biomass is calculated using the Chambers et al. (2001b) equation based on DBH, this pattern was also demonstrated in calculated biomass distribution, where 37.5, 24.4, and 18.9% of the TAGB was found in the medium tree size class for Manaus, Rio Branco, and Santarém, respectively (Fig. 2c). Basal area, which is also based on DBH (Fig. 2b), showed the same trends among sites. Estimated dry biomass in the year that the forest plots were

Fig. 2 Distribution of number of individuals (ha^{-1}), basal area (m^2 ha^{-1}) and biomass (Mg ha^{-1}) of trees in the permanent plots by diameter class. *Numbers in parentheses* are the percentage of the total

established was greatest (360 Mg ha^{-1}) in Manaus, smallest (190 Mg ha^{-1}) in Rio Branco, and 281 Mg ha^{-1} in Santarém. These values are within the range of values reported for other primary Neotropical forests (Brown et al. 1995; Gerwing and Farias 2000; Chave et al. 2001; Keller et al. 2001).

Table 2 Mean annual diameter growth increments in mm ± SE of the mean observed using dendrometer bands in the three permanent plots. Negative growth rates indicate a decrease in tree diameters during the period of study

	Manaus			Rio Branco		Santarém	
	2000	2001	2002	2001	2002	2000	2001
Diameter growth rate (mm year^{-1})	1.48±0.20	1.78±0.24	1.99±0.23	3.89±0.33	3.77±0.38	3.63±0.23	2.54±0.21
Minimum individual growth rate (mm year^{-1})	−0.4	−0.7	−0.3	−5.0	−14.5	−2.0	−5.9
Maximum individual growth rate (mm year^{-1})	8.6	9.8	8.6	49.6	44.4	19.3	36.2
Percentage of all individuals with negative growth rates	23%	19%	10%	9%	11%	12%	22%
Annual total precipitation (mm)	3,546	2,383	3,178	1,900	1,910	2,594	1,765
Number of dry season months (precipitation <100 mm month^{-1})	0	2[a]	3[a]	4	4	5[a]	6
Total precipitation in the dry season (mm)	–	96	305	285	240	107	232
Minimum monthly precipitation (mm)	126	48	72	44	2	3	17
Maximum monthly precipitation (mm)	736	294	536	472	345	362	314

[a]Months not consecutive

Differences in biomass are mainly related to both the frequency of individuals and their size. More than 80% of the individuals in all three areas were in the small (10–29.9 cm DBH) size class but this accounted for only 26.4–32.9% of total biomass in the three areas (Fig. 2). At Manaus 70.8% of the biomass was found in small and medium size classes, while in Rio Branco and Santarém this fraction represented only 56.2 and 45.3%, respectively. Giant trees (>100 cm DBH) occurred with a frequency of 0.6 individuals ha^{-1} in Manaus, 2.4 ha^{-1} Rio Branco, and 3.6 ha^{-1} in Santarém.

Brown et al. (1995) found that 50% of TAGB was found in trees larger than 60 cm DBH in a primary tropical forest in Rondônia. We found a similar result for Santarém (44.5% of TAGB in trees >60 cm DBH; Fig. 2), but not in the other two sites, where trees >60 cm DBH accounted for only 31.3% (Rio Branco) and 16.7% (Manaus) of TAGB.
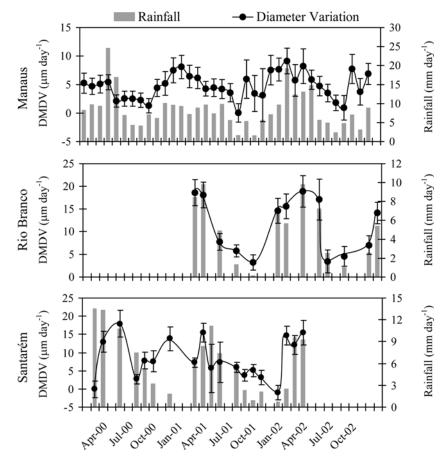
Growth rates

Mean annual growth increments derived from dendrometer measurements were highest in Rio Branco (3.9 mm year^{-1}), followed by Santarém (3.1 mm year^{-1}) and Manaus (1.7 mm year^{-1}) (Table 2). Growth rates were extremely variable, and differences in mean annual growth increment between Rio Branco and Santarém are not significant ($p=0.023$, where we define significance at

$p<0.001$). However, both sites had significantly higher growth rates than trees in Manaus ($p<0.001$).

Daily diameter variation was significant in all three areas and clearly was influenced by seasonality in precipitation (Fig. 3). Diameter variations were positively correlated with the precipitation in Manaus forest ($P=0.0001$) and Rio Branco forest ($P=0.0145$). In Santarém the correlation between mean daily diameter variation and precipitation was not significant when calculated for the entire period of measurement ($P=0.254$), but was significant when calculated considering only the year 2001 ($P=0.0152$). The differences between wet and dry season average diameter increments were 8.6, 19.5 and 19.0 μm day^{-1} in Manaus, Rio Branco and Santarém respectively. As noted earlier, seasonal differences may be overestimated if stem water contents increase from dry to wet season.

Interannual differences in growth rates for individual areas (Table 2) were not significant for Manaus and Rio Branco, but were significant ($P=0.0009$) for Santarém. At all sites, the largest trees (>50 cm DBH) showed the fastest growth rates and the smallest trees (10–30 cm DBH) the slowest growth rates ($P=0.028$ at Manaus, $P=0.048$ at Rio Branco and $P=0.0001$ at Santarém) (Fig. 4). When growth is expressed in terms of the per cent of diameter increment, the differences in growth among tree size classes are still significant. Large (>50 cm DBH) trees also showed the greatest seasonal variation, with higher-than-average growth rates in the wet season, and lower-than-average

Fig. 3 Daily mean diameter variation (*DMDV*) in μm ± 95% confidence interval, compared with mean precipitation accumulated (reported in mm day^{-1}) measured for the three areas

growth rates in the dry season. Trees in the 10–30 cm size class showed the least seasonal response.

Total biomass accumulation

Living trees in forest plots in Rio Branco and Santarém accumulated roughly 2.6 Mg C ha^{-1} year^{-1} through tree growth (2.61±0.08 and 2.59±0.64 Mg C ha^{-1} year^{-1}), significantly more than the forest plot in Manaus (1.92 ±0.39 Mg C ha^{-1} year^{-1}; Table 3). Interannual differences in annual carbon accumulation in live trees were large (up to 0.70 Mg C ha^{-1} year^{-1}, or ~40% of the mean) were significant in Manaus (P=0.0000), and Santarém (with a difference of 0.8 Mg C ha^{-1} year^{-1} between 2000 and 2001, 33% of the mean), but not in Rio Branco (differing by 0.1–0.2 Mg C ha^{-1} year^{-1} between 2001 and 2002). In all three sites, the smallest trees (10–30 cm DBH), which are ≥80% of the individuals, are responsible for a large fraction of the carbon accumulated annually through tree diameter increment (35–44% of the total in Manaus, and ~55% in Rio Branco and Santarém; Table 3). Individuals in the 30–50 cm size class accounted for roughly 37% of the annual C accumulated in living biomass in Manaus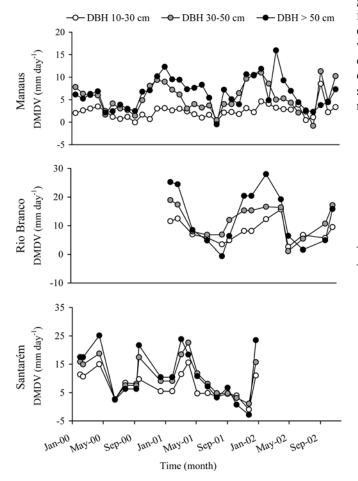, although this size class accounted for <30% of the C accumulated in the other areas. Trees with DBH >50 cm represent 15–18% of total carbon accumulated by living tree growth in Rio Branco, although in the other areas they account for 20–27% of annual C accumulation. These patterns of C allocation by size class were repeated in all available years of measurement (Fig. 5).

Live wood carbon balance

The C accumulation in living trees constitutes only part of the live wood carbon balance. When recruitment and mortality data are considered along with changes in tree diameter, the live wood pool in the Manaus forest plot is losing C at a rate of 0.15 Mg C ha^{-1} year^{-1} (Rocha 2001), while the Rio Branco (this work) and Santarém (Rice et al. 2004) forest plots are accumulating C in the live aboveground biomass at rates of 1.0–1.5 Mg C ha^{-1}-year^{-1}.

Discussion

A number of factors may be responsible for the significant differences we observed in diversity, biomass structure and growth rates among sites, including: (1) length and intensity of the dry season; (2) light availability; (3) differences in soil characteristics (i.e., nutrient availability, water holding capacity, soil texture, etc); (4) differences in disturbance (mortality rates, size of clearings, etc.) that can occur over the short- or the long-term; (5) differences in species composition (mean wood density, intrinsic growth rates); and (6) hydrologic regime.

Fig. 4 Daily mean diameter variation (*DMDV*) in μm by diameter class (10–29.9, 30–49 and >50 cm)
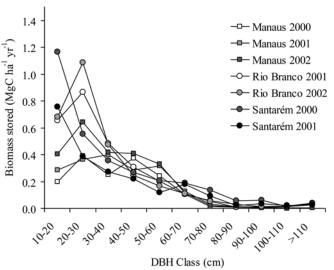

Fig. 5 Distribution of annual carbon accumulation in living vegetation among diameter classes for the years of measurement

Table 3 Mean annual carbon accumulation in living tree biomass Mg C ha^{-1} year^{-1} and as percentage of the total accumulated in each size class in Manaus, Rio Branco and Santarém. Values in parentheses are percentages

Size class (cm)	Manaus			Rio Branco		Santarém	
	2000	2001	2002	2001	2002	2000	2001
10–30	0.6 (37.2)	0.7 (35.3)	1.0 (44.4)	1.4 (52.9)	1.5 (57.3)	1.7 (56.6)	1.2 (53.5)
30–50	0.6 (39.2)	0.7 (37.3)	0.8 (35.0)	0.8 (29.4)	0.7 (27.3)	0.6 (20.5)	0.5 (23.1)
>50	0.4 (23.6)	0.7 (27.4)	0.5 (20.6)	0.5 (17.6)	0.4 (15.2)	0.7 (23.0)	0.5 (23.4)
Total	1.6	2.1	2.3	2.7	2.6	3.0	2.2

Dry season length

As noted previously, the sites with longer dry seasons, Santarém and Rio Branco, had the smallest stem frequency, diversity (species ha^{-1}) and the highest annual growth increment in trees, while the site with the shortest dry season, Manaus, had the highest stem frequency, highest diversity and smallest growth increment. Steeg et al. (2000) suggest that species diversity is strongly influenced by the duration of the dry season, and other studies have shown a relationship between total rainfall and diversity in Neotropical regions (Phillips et al. 1994; Gentry and Dodson 1987; Gentry 1988; Condit et al. 2000).

Tree diameter increment at all sites showed a strong relationship with the amount of seasonal rainfall. Interannual variation in C allocated to growing stems did not show relationships with precipitation, either between years at one site, or among different sites in a given year, although the data in Rice et al. (2004) suggests that there may be a correlation between total annual precipitation and C uptake in living trees.

Light availability

Differences in vertical canopy structure among the three sites result in differences in the attenuation of light through the canopy, and thereby directly affect photosynthesis, and under some conditions, the amount of C allocated to growth of woody tissue (Rijkers et al. 2000; Körner 2004). In Manaus, which has few giant emergent trees and a canopy of relatively even height, less light can reach the forest floor than in Rio Branco and Santarém, areas with a more stratified canopy that allows more light penetration. Light availability may also explain the tendency for slowest growth rates to be observed in the smallest trees, since these are likely to experience the least light (and perhaps highest water stress in dry periods).

Soil properties

Although the soils in all three sites are dominated by Oxisols with low phosphorous content, some differences in soil properties exist. Manaus, the site with slowest growth, also had the lowest amount of total base cations (2.1–6.5; Telles et al. 2003; Willian Flores, SETEM, personnal communication) of the three sites. On the other hand, Rio Branco, with relatively fast growth rates, had

soils with the lowest organic matter content, cation exchange capacity and base saturation. Therefore, no obvious link between soil properties and growth rates can be found for the sites in this study.

Disturbance

In Rio Branco and Santarém the annual accumulation of C (biomass) in living trees was ~30% greater than in Manaus. Only up to a quarter (but clearly not all) of this difference could be due to uncertainties in allometry estimates (which have been corrected for in Rio Branco but not in Santarém, Malhi et al. (2004) found the same patterns of C accumulation, with 1.5–2.5 Mg C ha^{-1} year^{-1} in the central Amazonia forest and 2.2–2.7 Mg C ha^{-1} year^{-1} near the our site in Santarém and 2.4–4.2 Mg C ha^{-1} year^{-1} in a forest in south Peru. One potential explanation for the much higher growth rates in these lower-biomass forests might have to do with response to previous disturbance. The period of data collection for our study occurred after a severe drought associated with what many consider the strongest El Ninõ-Southern Oscillation (1997–1998 ENSO) event of this century (Marengo and Tomasella, 1998; MacPhaden 1999), and which decreased precipitation for the entire year (Ronchail et al. 2002). Mortality rates covering the years spanning this event showed an increase of as much as 70% in a central Amazon forest near Manaus (Williamson et al. 2000; Körner 2003; Clark 2004). In tropical forests of Indonesia, the rate of morality in the 1997–1998 ENSO event increased from 1–3% (Phillips and Gentry 1994a) to approximately 10% (Kinnaird and O'Brien 1998). Recovery from a large mortality event would be associated with changes in forest structure and could explain increased growth rates (Williamsom et al. 2000). These effects might be amplified in areas that experience a longer dry season such as Rio Branco and Santarém, though we have no mortality estimates for the period preceding our study in these areas. The pool of dead wood in the forest plot we studied in Santarém is larger than would be expected at steady state given observed mortality rates (Rice et al. 2004; Saleska et al. 2003), which might reflect recent disturbance. In addition, human disturbance through selective logging and extractive management may have affected the sites in Santarém and Rio Branco to a larger degree than the Manaus Jacaranda plot.

Species composition/Intrinsic growth rates

Growth rates in our tropical forest sites were dependent on size, with largest trees showing the highest absolute growth rates, consistent with previous studies. For example, Clark and Clark (1999) showed a positive correlation between annual basal area increment and stem diameter in a lowland Neotropical rain forest in Costa Rica. Da Silva et al. (2002) showed that mean annual increment for the largest trees (DBH>50 cm) was significantly greater than the other trees (DBH<50 cm). According to Hubbel et al. (1999), this tendency of larger individuals to have greater diameter increment is related with greater photosynthetic activity of those individuals, which generally dominate the sunlit forest canopy.

Growth rates measure changes in diameter (or circumference), which are related to changes in biomass/C inventory by use of an allometric equation. If the allometric equation is based on locally harvested trees, errors are minimized. As already discussed, the fact that we are applying the equation of Chambers et al. (2001a,b) which was developed in the Central Amazon to forests with clearly different structure introduces significant error in our estimates. These errors could be due to differences in average wood density for forest stands, or to changes in average tree height among our three studied areas. Chambers et al. (2001b) demonstrated that allometric models developed in Manaus and at a drier site in the Brazilian state of Pará were quite similar, suggesting that regional shifts in mean wood density, at least in some cases, is not a major concern. Baker et al. (2004) suggest that forests in the central and eastern Amazon have similar stand wood densities. We thus have applied the Chambers et al. (2001b) equation to data in Santarém without correction. However, allometric equations based on harvested trees in Amazon forests are quite limited. Though there are likely some regional differences in mean stand level wood density, this factor remains poorly characterized (Williamson 1984), though studies are underway to improve the database of wood density (Baker et al. 2004). The large differences in biomass increment between Manaus and Rio Branco/Santarém forests exceed the suggested density correction to allometry (Table 3).

Hydrologic regime

Plant water availability can affect not only growth rates but also the vertical structure of the forest. (Porporato et al. 2001; Dunisch et al. 2002). Forest structure is determined by disturbance history, radial growth rates of individual plants and by their competitive interactions (Niels and Anten 2001), all of which may be strongly influenced by climate (Clark and Clark 1994; Roderick et al. 2001). According to Porporato et al. (2001), physiological processes such as photosynthesis and nutrient transfer are reduced as the stores of water available to the plant decrease. Tree growth can therefore be limited more frequently by lack of water than by other factors (Nepstad et al. 2002), influencing not only the diameter increment growth, but also how trees are distributed in the forest. Too much precipitation can also affect tree growth rates. Saturated soils limit root respiration and slow photosynthesis. In areas experiencing high annual rainfall, such as the central Amazon, soils can be temporarily inundated. Clouds associated with rain can also influence photosynthesis rates. Our Manaus site experienced its smallest diameter increment in the year 2000, when annual precipitation was ~55% greater than normal.

In this study, the area subjected to the shortest dry season (and presumably the least water stress) had different canopy structure, with the majority of trees of small to medium size (<50 cm DBH), and the slowest annual growth rates. Water availability may influence forest structure and biomass in the longer term, through factors like species composition, while shorter-term differences in growth rate may be more related to recent disturbance.

The residence time of carbon in trees

The site with the largest biomass in this study, Manaus, was also the site with slowest growth rates. If we assume the observed average diameter growth increment of 1.7 mm $year^{-1}$ for this site is constant, a tree of average diameter (396 mm) would take 240 years to reach that size. For the Rio Branco and Santarém sites with annual diameter increment of 3.9 and 3.1 mm $year^{-1}$, respectively, the average diameter trees of 445 and 559 mm diameter would both take ~140 years to reach that size. This tendency of trees in Manaus to be on average older than those of Rio Branco and Santarém is confirmed by radiocarbon analyses of tree age in the same three sites (Vieira 2003; Vieira et al, unpublished data). The same tendency was verified by Malhi et al. (2004) to several sites in Amazonia. Mean tree ages predicted for Manaus are similar to those predicted by the model of Chambers et al. (2000), but are significantly longer than those used by other models of carbon dynamics in tropical forests. Our estimates of tree growth, recruitment and mortality in Manaus suggest that this forest is in close to C balance, in contrast to the Rio Branco and Santarém forests, which appear to be accumulating C in living trees. Tree ages derived using growth rates that could be responding to recent disturbance in Rio Branco and Santarém, which could lead to underestimation of mean tree age at these sites.

Interannual differences in C allocated to live wood growth measured in this study were large, up to 0.9 Mg C ha^{-1} $year^{-1}$, or 40% of total C accumulation through diameter increment each year. Site to site and year to year variations in tree diameter increment can reflect several factors, and are not simply differences in precipitation from area or year to another.

Conclusions

Terra-firme tropical forests are not all equal in biomass, structure and function. The Central Amazonian forest we studied near Manaus had higher biodiversity, biomass and C stocks, but lower growth rates than two other forests experiencing a more pronounced dry season. Higher C stocks, combined with slower growth rates, indicate that trees in this Central Amazon forest are on average older than those at the other sites, and older than values of tree mean age presently used in models of tropical forest C dynamics.

Growth rates were highest in the largest trees, and large trees represented a greater number of individuals and biomass in the Rio Branco and Santarém sites. Diameter increment changes in large trees varied seasonally with changes in precipitation, with less apparent growth during the dry season, and greater rates during the wet season. These seasonal differences may be confounded by variation in stem water content. Seasonal variations were less pronounced in smaller size classes.

Correction for recruitment and mortality resulted in the conclusion that live wood is approximately in steady state in the Manaus forest, but accumulating approximately 1.5 Mg C ha^{-1} year^{-1} in the Rio Branco and Santarém sites. It is important to note that carbon accumulation in tree trunks does not mean that the whole forest is acting as a carbon sink. Living trees are only one factor in the overall forest C balance. These estimates allow us to determine C balance in living wood biomass; site carbon balance will depend on additional factors: the amount and decomposition rate of dead wood, the production and decay of litter and fine roots, and changes in the stocks of soil organic carbon. For example, based on observations of dead wood inventory and decomposition rates, Rice et al. (2004) and Saleska et al. (2003) infer that the entire wood (live + dead) C pool is losing C to the atmosphere at the Santarém site. Telles et al. (2003) recently showed that soils may either accumulate or lose C at rates approaching 1 Mg C ha^{-1} year^{-1} following changes in litterfall or disturbance.

Because live wood plays a key role in both overall C balance and interannual variation, the large variability of biomass stocks and growth rates reported here for three Amazonian forest sites demonstrates that more work is needed to understand the sources of this variation.

References

Araújo TM, Higuchi N, Carvalho JA (1999) Comparison of formulas for biomass content determination in a tropical rain Forest site in the states of Pará, Brazil. For Ecol Manage 117:43–52

Baker TR, Phillips OL, Malhi Y, Almeida A, Arroyo L, Fiori A, Killeen T, Laurence S, Laurencec W, Lewis S, Lloyd J, Monteagudo A, Neill D, Patiño S, Pitman N, Silva N, Martínez R (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biol (in press)

Bernoux M, Carvalho MDS, Volkoff B, Cerri CC (2002) Brazil's soil carbon stocks. Soil Sci Soc Am 66:888–896

Braga PIS (1979) Subdivisão fitogeográfica, tipos dee vegetação, conservação e inventário florístico da floresta amazônica. Acta Amazonica 9:53–80

Brown IF, Martinelli LA, Wayt Thomas W, Moreira MZ, Cid Ferreira CA, Victoria RL (1995) Uncertainty in the biomass of Amazonian forest: an example from Rondônia, Brazil. For Ecol Manage 75:175–189

Camargo PB, Trumbore SE, Martinelli LA, Davidson EA, Nepstad DC, Victoria RL (1999) Soil carbon dynamics in regrowing forest of eastern Amazonia. Global Change Biol 5:693–702

Chambers JQ, Higuchi N, Schimel J, Ferreira LV, Melack JM (2000) Decomposition and carbon cycling of dead trees in tropical forests of central Amazon. Oecologia 122:380–388

Chambers JQ, Higuchi N, Tribuzy ES, Trumbore SE (2001a) Carbon sink for a century. Nature 410:429

Chambers JQ, Santos J, Ribeiro RJ, Higuchi N (2001b). Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. For Ecol Manage 152:73–84

Chauvel A, Lucas Y, Boulet R (1987) On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. Experientia 43:234–241

Chave BR, Dubois MA (2001) Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. J Trop Ecol 17:79-96

Clark DA (2004) Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. Phil Trans R Soc London B Biol Sci DOI 10.1098/rstb.2003.1426

Clark DA, Clark DB (1994) Climate-induced annual variation in canopy tree growth in Costa Rica tropical rain forest. J Ecol 82:865–872

Clark DB, Clark DA (1996) Abundance, growth and mortality of very large trees in neotropical lowland rain forest. For Ecol Manage 80:235–244

Clark DA, Clark DB (1999) Assessing the growth of tropical rain forest trees: Issues for forest modeling and management. Ecol Appl 9:981-997

Condit R, Ashton PS, Baker P, Saravudh B, Savithri G, Gunatilleke N, Hubbel SP, Foster RB, Itoh A, Lafrankie JV, Lee HS, Losos E, Monokaran N, Sukumar R, Yamakura T (2000) Spatial patterns in the distribution of tropical tree species. Science 288:1414–1418

Curtis JT, McIntosh RP (1950) The interrelationships of certain analytic and synthetic phytosociological characters. Ecology 31:434–455.

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. Science 263:185–190

Dunisch O, Morais RR (2002) Regulation of xylem sap flow in an evergreen, a semi-deciduous, and a deciduous Meliaceae species from the Amazon. Trees 16:404–416

Elsenbeer H, Lack A (1997) Hydrological pathways and water chemistry in Amazonian rain forests In: Anderson MG, Brooks SM (eds) Advances in hillslope processes, vol 2. Wiley, New York, pp 939–959

Ferraz J, Ohta S, Sales PC (1998) Distribuição dos solos ao longo de dois transectos em floresta primária ao Norte de Manaus (AM). In: Higuchi N, Campos MAA, Sampaio PTB, Santos, J (eds) Pesquisas Florestais para a conservação da floresta e reabilitação de áreas degradadas da Amazônia. Manaus, pp 109–143

Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281:237–240

FRA FAO (2001) Forest resources assessment food and agriculture organization of the United Nations 2000: tropical countries. FAO Forestry Paper 140, Rome, pp 287–291

Gentry AH (1988) Change in plant community diversity and floristic composition on environmental and geographical gradients. Ann Mo Bot Gard 75:1–34

Gentry AH, Dodson CH (1987) Diversity and biogeography of neotropical vascular epiphytes. Ann Mo Bot Gard 74:205–233

Gerwing JJ, Farias DL (2000) Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. J Trop Ecol 16:327–335

Grace J, Lloyd J, McIntyre A, Miranda A, Meir P, Miranda H, Moncrieff J, Massheder J, Wright I, Gash J (1995a) Fluxes of carbon-dioxide and water-vapor over an undisturbed Tropical forest in south-west Amazonia. Global Change Biol 1:1–12

Grace J, Lloyd J, McIntyre J, Miranda A, Meir P, Miranda H, Nobre C, Moncrieff J, Massheder J, Malhi Y, Wright I, Gash J (1995b). Carbon-dioxide uptake by an undisturbed tropical rain-forest in southwest Amazonia, 1992–1993. Science 270:778–780

Higuchi N, dos Santos J, Ribeiro RJ, Freitas JV, Vieira G, Cöic A, Minette LJ (1997) Crescimento e Incremento de uma Floresta Amazônica de Terra-Firme Manejada. In: Biomassa de nutrientes florestais. INPA/DFID, Manaus, pp 89–132

Higuchi N, dos Santos J, Vieira G, Ribeiro RJ, Sakurai S, Ishizuka M, Sakai T, Saito S (1998) Análise Estrutural da Floresta Primária da Bacia do Rio Cuieira, ZF-2, Manaus-AM, Brazil. In: Higuchi N, Santos J, Ribeiro RJ, Minette L e Biot Y (eds) Biomassa da parte aérea da vegetação da floresta tropical úmida de terra-firme da Amazônia brasileira. Acta Amazonica 28:153–166

Houghton RA, Skole DL, Nobre CA, Hackler JL, Lawrence KT, Chomentowski WH (2000) Annual fluxes of carbon from deforestation and regrowth on the Brazilian Amazon. Nature 403:301–304

Hubbel SP, Foster RB, O'Brien ST, Harms KE, Condit R. Weschsler B, Wrigth S, Loo de Lao S (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. Science 283:554–557

INMET (2001) Instituto Nacional de Meteorologia http://www.inmet.gov.br

Jardim FCS, Hosokama RT (1986) Estrutura da floresta equatorial de terra-firme. Acta Amazônica 18:211–220

Keeland BD, Sharitz RR (1993) Accuracy of tree growth measurements using dendrometer bands. Can J For Res 23:2454–2457

Keller M, Palace M, Hurtt G (2001) Biomass estimation in the Tapajós National Forest, Brazil. Examination of sampling and allometric uncertainties. For Ecol Manage 154:371–382

Ketterings QM, Coe R, Noordwijk M, van Ambagau Y, Palm CA (2001) Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. For Ecol Manage 146:199–209

Kinnaird MF, O'Brien TG (1998) Ecological effects of wildfire on lowland rainforest in Sumatra. Conserv Biol 12:954–956

Körner C (2003) Slow in, Rapid out—Carbon flux studies and Kyoto targets. Science 300:1242–1243

Körner C (2004) Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. Phil Trans R Soc London B. DOI 10.1098/rstb.2003.1429

Liebmann B, Marengo JA (2001) Interannnual variability of the rainy season and rainfall in the Brazilian Amazon Basin. J Climate 14:4308–4318

Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press. Princeton

Magurran AE (2003) Measuring biological diversity. Blackwell, Malden

Malhi Y, Nobre AD, Grace J, Kruijt B, Pereira MGP, Culf A, Scott S (1998) Carbon dioxide transfer over a Central Amazonian rain forest. J Geophys Res 103:1593–1612

Malhi Y, Meir P, Brown S (2002) Forests, carbon and global climate. Phil Trans R Soc A 360:1567–1591

Malhi Y, Phillips OL, Baker T, Almeida S, Alvarez E, Arroyo L, Chave J, Czimczik C, Fiore A, Higuchi N, Killeen T, Laurencec S, Laurence W, Lewis S, Montoya L, Monteagudo A, Neill D, Vargas P, Patiõ S, Pitman N, Quesada C, Salomão R, Silva N, Lezama A, Martínez R, Terborgh J, Vincenti B, Lloyd J (2004) Above ground coarse wood productivity and net primary productivity of 104 Neotropical forest plots. Global Change Biol (submitted)

Marengo JA, Nobre CA (2001) General characteristics and variability of climate in the Amazon Basin and its links to the global climate system. In: McClain ME, Victoria RL, Richey JE (eds) The biogeochemistry of the Amazon Basin, Oxford University Press, New York, pp 17–41

Marengo JA, Tomasella J (1998) Trends in streamflow and rainfall in tropical South America: Amazonia, eastern Brazil, and north-western Peru. J Geophys Rew-Atmos 103:1775–1783

Martins FR, Santos FAM (1998) Técnicas usuais de estimativa de biodiversidade. Revista Holos 236–267 Edição Especial

McPhaden MJ (1999) Genesis and evolution of the 1997-1998 El Niño. Science. 283:950–954

Melillo JM, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL (1993) Global climate-change and terrestrial net primary production. Nature 363:234–240

Nelson BW, França MB. Nogueira ME, Oliveira ACA (2004) Adapting allometry for biomass estimation in the Amazonian arc of deforestation. Global Change Biol (submitted)

Nepstad DC, Carvalho CR, Davidson EA, Jipp PH, Levebvre PA, Negreiros GH, Silve ED, Stone TA, Trumbore SE, Vieira S (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forest and pasture. Nature 372:666–669

Nepstad DC, Moutinho P, Dias MB, Davidson E, Cardinot G, Markewitz D, Figueiredo R, Vianna N, Chambers J, Ray D, Guerreiros JB, Lefebvre P, Sternberg L, Moreira M, Barros L, Ishida FY, Tohlver I, Belk E, Kalif K, Schwalbe K (2002) The effects of partial through fall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon. For J Geophys Rew-Atmos 107:8085 doi:10.1029/2001JD000360

Niels PR, Anten TH (2001) Limitations on photosynthesis of competing individuals in stands and the consequences for canopy structure. Oecologia 129:186–196

NuRMA (2002) Núcleo de Monitoramento Agroclimático. BHBrasil – Balanços Hídricos Climatológicos de 500 localidades brasileiras. http://ce.esalq.usp.br/dce/nurma.htm

Oliveira AA, Nelson BW (2001) Floristic relationship of terra-firme forests in the Brazilian Amazon. For Ecol Manage 146:169–179

Parrota JA, Francis JK, Almeida RR (1995) Trees of the Tapajós: a photographic field guide. General Technical Report IITF-1. USDA, Rio Piedras, Puerto Rico

Phillips OL, Gentry AH (1994a) Increasing turnover through time in tropical forests. Science 263:954–958

Phillips OL, Hall P, Gentry AH, Sawyer SA, Vasquez R (1994) Dynamics and species richness of tropical rain forests. Proc Natl Acad Sci USA 91:2805–2809

Phillips OL, Malhi Y, Higuchi N, Laurence WF, Núñes PV, Vásquez RM, Laurencec SG, Ferreira LV, Stern M, Brown S, Grace J (1998) Change in the carbon balance of tropical forest: evidence from long-term plots. Science 282:439–442

Phillips OL, Malhi Y, Vinceti B, Baker T, Lewis SL, Higuchi N, Laurance WF, Vargas PN, Martinez RV, Laurance S, Ferreira LV, Stern M, Brown S, Grace J (2002) Changes in growth of tropical forests: evaluating potential biases. Ecol Appl 12:576-587.

Porporato A, Laio F, Ridolfi L, Rodriguez-Iturbe I (2001) Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress. III. Vegetation water stress. Adv Water Resour 24:725–744

Potter CS, Randerson J, Field C, Matson P Vitousek PM, Mooney HA, Klooster S (1993) Terrestrial ecosystem production: a process model based on global satellite and surface data. Global Biogeochem Cycles 7:811–841

Rice AH, Pyle EH, Saleska SR, Hutyra L, Palace M, Keller M, Camargo PB, Portilho K, Marques DF, Wofsy SC (2004) Carbon balance and vegetation dynamics in an old-growth Amazonian forest. Ecol Appl (in press)

Rijkers T, Pons TL, Bongers F (2000) The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. Funct Ecol 14:77–86

Rocha RM (2001) Taxas de recrutamento e mortalidade da floresta de terra-firme da bacia do Rio Cuieiras na região de Manaus-AM. Mestrado INPA/FUA, Manaus, Brazil

Roderick ML, Farquhar GD, Berry SL, Noble IR (2001) On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. Oecologia 129:21–30

Ronchail J, Cochonneau G, Molinier M, Guyot JL, Chaves AGD, Guimaraes V, de Oliveira E (2002) Interannual rainfall variability in the Amazon basin and sea-surface temperatures in the equatorial Pacific and the tropical Atlantic Oceans. Int J Clim 22:1663–1686

Saleska SR, Miller SD, Matross DM, Goulden ML, Wofsy SC, da Rocha HR, de Camargo PB, Crill P, Daube BC, de Freitas HC, Hutyra L, Keller M, Kirchoff V, Menton M, Munger W, Pyle EH, Ricee AH, Silva H (2003) Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. Science 302:1554–1557

Salimon CI, Brown IF, Stone TA (2004) Diminishing secondary and primary forests in Acre State, Brazil, Western Amazonia. Remote Sens Environ (in press)

Schimel DS (1995) Terrestrial ecosystems and carbon cycle. Global Change Biol 1:77–91

da Silva RP, dos Santos J, Tribuzi, ES, Chambers JQ, Nakamura S, Higuchi N (2002) Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. For Ecol Manage 166:295–301

Silveira M (2001) A floresta aberta com bamboo no sudoeste da Amazônia: Padrões e processos em múltiplas escalas. DF. Tese, Universidade de Brasília, Brasilia

Sombroek W (2001) Spacial and temporal patterns of Amazon rainfall. Ambio 30:388–396

Steeg HT, Sabatier D, Castellanos H, Van Andel T, Duivenvoorden J, Oliveira AA, Ek R, Lilwah R, Maas P, Mori S (2000) An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. J Trop Ecol 16:801-828

Telles EDC, de Camargo PB, Martinelli LA, Trumbore SE, da Costa ES, Santos J, Higuchi N, Oliveira RC (2003) Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia. Global Biogeochem Cycles 17:doi 10.1029/2002GB001953

Trumbore SE, Davidson EA, Camargo PB, Nepstad DC, Martinelli LA (1995) Belowground cycling of carbon in forest and pastures of eastern Amazonia. Global Biogeochem Cycles 9:515–528

Vetter RE, Botosso PC (1989) El Niño may affect growth behavior of Amazonian tree. GeoJournal 19:419–421

Vieira SA (2003) Mudanças globais e tasa de crescimento arbóreo na Amazônia. Tese, CENA/USP, Piracicaba

Williamson GB (1984) Gradients in wood specific-gravity of trees. Bull Torrey Bot Club 111:51–55

Williamson GB, Laurence WF Oliveira AA, Delamônica P, Gascon C, Lovejoy TE, Pohl L (2000) Amazonian tree mortality during the 1997 El Niño drought. Conserv Biol 14:1538–1542