# Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests

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## Abstract

The allocation and cycling of carbon (C) within forests is an important component of the biospheric C cycle, but is particularly understudied within tropical forests. We synthesise reported and unpublished results from three lowland rainforest sites in Amazonia (in the regions of Manaus, Tapajós and Caxiuanã), all major sites of the Large-Scale Biosphere–Atmosphere Programme (LBA). We attempt a comprehensive synthesis of the C stocks, nutrient status and, particularly, the allocation and internal C dynamics of all three sites. The calculated net primary productivities (NPP) are $10.1 \pm 1.4\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ (Manaus), $14.4 \pm 1.3\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ (Tapajós) and $10.0 \pm 1.2\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ (Caxiuanã). All errors bars report standard errors. Soil and leaf nutrient analyses indicate that Tapajós has significantly more plant-available phosphorus and calcium. Autotrophic respiration at all three sites ($14.9$–$21.4\,\mathrm{Mg\,C\,ha\,yr^{-1}}$) is more challenging to measure, with the largest component and greatest source of uncertainty being leaf dark respiration. Comparison of measured soil respiration with that predicted from C cycling measurements provides an independent constraint. It shows general good agreement at all three sites, with perhaps some evidence for measured soil respiration being less than expected. Twenty to thirty percent of fixed C is allocated belowground. Comparison of gross primary productivity (GPP), derived from ecosystem flux measurements with that derived from component studies (NPP plus autotrophic respiration) provides an additional crosscheck. The two approaches are in good agreement, giving increased confidence in both approaches to estimating GPP. The ecosystem carbon-use efficiency (CUEs), the ratio of NPP to GPP, is similar at Manaus ($0.34 \pm 0.10$) and Caxiuanã ($0.32 \pm 0.07$), but may be higher at Tapajós ($0.49 \pm 0.16$), although the difference is not significant. Old growth or infertile tropical forests may have low CUE compared with recently disturbed and/or fertile forests.

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## Introduction

In our increasing understanding of the cycling of carbon (C) within the biosphere and its current and potential

response to global environmental change, much attention has focussed on understanding and modelling photosynthesis and its limitation by nutrients and water. However, the *allocation* of the products of photosynthesis between metabolic activity, short-lived tissues and long residence woody biomass, is an equally important but much less-studied feature (DeLucia *et al.*, 2007; Litton *et al.*, 2007). Poor understanding of allocation and simplified model assumptions constrain our ability to predict the effects of global change on the C dynamics of the biosphere.

Tropical forests play a particularly important role in global C cycle (Malhi & Grace, 2000), but are generally understudied because of challenging logistics and remoteness from sources of scientific funding. Until recently, very few tropical forests have had their C dynamics examined in detail with modern techniques (Chambers *et al.*, 2004). The Large-Scale Biosphere–Atmosphere (LBA) programme in Amazonia has recently conducted such studies at a number of sites in Brazilian Amazonia, but the work has been carried out across a number of research groups, even at the same site. In this paper, we synthesise results on the C stocks, nutrient stocks and particularly the internal C allocation in forests close to three major LBA eddy covariance flux towers in the regions of Manaus, Tapajós and Caxiuanã. The ultimate aim is to compare component estimates of C cycling with integrated measurements from soil respiration studies and flux towers, thereby understanding the internal C allocation of these forest sites and evaluating the feasibility and completeness of the 'bottom-up' measurement approach to be applied to other sites where flux towers do not exist.

## Materials and methods

### Study sites

We focus on three LBA sites that combine flux tower data with extensive biometric studies: Manaus, Tapajós and Caxiuanã. The location of the study regions in the context of Amazonia, and the distribution of study sites within each study region are mapped in Fig. 1.

At Manaus (Fig. 1b) our main focus is the K34 flux tower (Araujo *et al.*, 2002), and the various studies that have been conducted in its vicinity. Flux data from the nearby C14 flux tower (Malhi *et al.*, 1998) are also reported. The landscape in this region consists of a low plateau ($\sim 90$ m a.s.l.) usually hosting terra firme forest on clay-rich ferralsols (FAO soil taxonomy) or oxisols (USDA taxonomy) extensively dissected by river valleys ($\sim 50$ m a.s.l.) hosting lower biomass forest on frequently waterlogged podzols (FAO)/spodosols (USDA). The local landscape is approximately evenly divided between

plateaux, slopes and valley bottoms. Key forest plots in the area are the three 1 ha 'Bionte' plots on the plateaux providing annual census data since 1989, and the two 5 ha (20 m × 2500 m) 'Jacaranda' transect plots that drape across the plateau–valley landscape. Some tree dynamics data from the nearby, extensive and long-running Biological Dynamics of Forest Fragments Project (BDFFP) project are also reported. The two eddy flux towers at Manaus (K34 and C14) have footprints that encompass this plateau–valley mosaic.

At Tapajós (Fig. 1c), our main focus is the km 67 flux tower (Saleska *et al.*, 2003; Hutyra *et al.*, 2007) and its vicinity. The landscape consists of a flat high plateau ($\sim 200$ m a.s.l.) with a deep water table, and very few surface water-courses. The soils are heavy Belterra clay ferralsols (FAO)/oxisols (USDA) interspersed with sandier patches. The key plots are four 1 ha transects established in 1999 immediately to the east of the tower (Rice *et al.*, 2004; Pyle *et al.*, 2008), along with other plots further south at km 72 and km 117 (Pyle *et al.*, 2008). The soils types in the footprint of the km 67 tower are approximately 68% clay or clay loam, 32% sand or sandy loam (Silver *et al.*, 2000) Longterm plot data from km 117 (collected by Natalino Silva) are also reported. A throughfall exclusion experiment is situated $\sim 5$ km from the flux tower (Nepstad *et al.*, 2002), and data from the control 1 ha plot and the predrought plot are also reported.

At Caxiuanã (Fig. 1d), the flux tower is situated on a low terra firme site ($\sim 15$ m a.s.l.) towards the mouth of the Amazon, in a region dissected by relatively broad, slow-flowing river valleys (a legacy of early Holocene sea-level rise). Soils are clay-rich ferralsols/oxisols in the terra firme regions occasionally interspersed with acrisols (FAO)/ultisols (USDA), and grading to sandy podzols/spodosols in the river valleys. The tower footprint is predominantly over clay ferrasols. A throughfall exclusion plot is situated approximately 2 km to the south of the flux tower, and there are a number of forest plots in the region installed by Samuel Almeida.

In their analysis of aboveground (AG) coarse wood productivity (AGCWP) across Amazonia, Malhi *et al.* (2004) noted that the forests on oxisols close to the main Amazon river in Eastern Amazonia were amongst the least dynamic and productive in the region. All three sites here are likely to fall into that category. Hence, care should be taken when making inferences from these sites to the wider Amazon region.

### Methods and approach

This paper reviews and interprets data available from various LBA studies, and thereafter provides a synthesis of the results. This is a broad synthesis and for reasons of brevity, we do not dwell on the methodologies for each
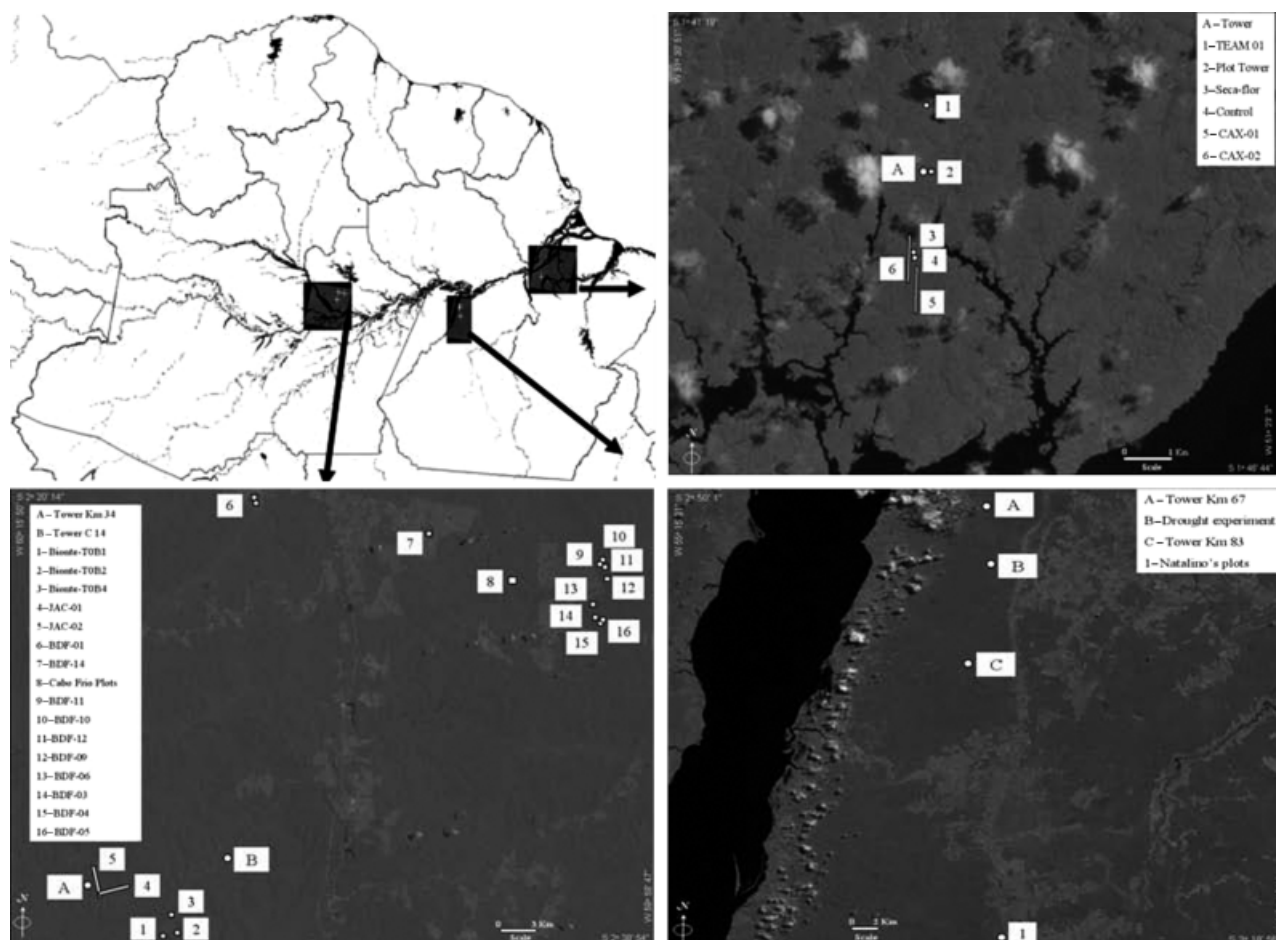
**Fig. 1** Location of the study sites. (a) The study regions in the context of Amazonia (b) The Caxiuanã site (c) The Manaus site (d) The Tapajós site. Field plots are assigned numbers and tower locations are assigned letters.

measurement, except where they are important in explaining differences between studies; the reader is referred to the original papers for detailed descriptions of the methodologies. We try and adopt the nomenclature suggested by Litton *et al.* (2007) where possible, and point out where our approach and nomenclature differs.

Because of the varied nature of the measurements from each site, we have adopted the approach of reviewing results from each approach in conjunction with discussing methodologies. In most sections, the results are presented at the start in a summary table, followed by a brief discussion and explanation of how a weighted average value was calculated for the synthesis table. A more detailed presentation of the methods and methodological differences is provided in the Supporting information. In 'Synthesis', we distil and summarise these results to present a direct and comprehensive comparison of the C cycle at all three sites. In compiling a summary value for a variable, we often average across several reported studies. For this averaging, we weight each study according to the area of the study plot, multiplied by the square root of the census period in years. Hence, spatially extensive or longer-term studies are given greater weighting, but spatial coverage is weighted more highly than temporal duration. All uncertainty estimates are reported as standard errors assuming normal distributions, unless stated otherwise. Where the original study only gives 95% confidence limits, we assume a normal distribution and estimate the standard error as (95% CI)/1.96. In all calculations, uncertainties are propagated by quadrature of absolute errors for addition and subtraction, and quadrature of relative errors for multiplication and division, with appropriate weighting for size and duration of each study (explained in greater depth in the Supporting information). This assumes that uncertainties can be considered to be independent and normally distributed. All results are reported in $Mg\,C\,ha^{-1}$ (for stocks) and $Mg\,C\,ha^{-1}\,yr^{-1}$ (for fluxes). $1\,Mg\,C\,ha^{-1}\,yr^{-1}$ is equal to $100\,g\,C\,m^{-2}\,yr^{-1}$, or $0.264\,\mu mol\,C\,m^{-2}\,s^{-1}$.

## Results

### C stocks (Table 1)

A selection of reported values of C stocks at each site are listed in Table 1, and summarised in Fig. 2.

AG live biomass is highest at Caxiuanã, slightly lower on the Manaus plateau, and lowest at Tapajós km 67 and in the Manaus valley bottoms. Some of these differences are reflected in forest structure: Caxiuanã has a greater proportion of large trees, Manaus much less. All these studies applied the allometric equation of Chambers *et al.* (2001a), in all cases except Tapajós modified by species-specific densities as applied by Baker *et al.* (2004).

Coarse woody debris (CWD) has been measured at Manaus and Tapajós, and is much greater at multiple sites across Tapajós. The CWD stocks at Tapajós appear to be in disequilibrium, and in combination with the low biomass, this suggests that the Tapajós local region underwent a recent and widespread major disturbance (Rice *et al.*, 2004; Pyle *et al.*, 2008). CWD has not been measured at Caxiuanã, but can be estimated by taking estimates of mortality biomass inputs and dividing by a wood decay constant, $k_{\text{wood}}$, of $0.16 \pm 0.04$, producing values very close to those observed at Manaus ($15.3 \pm 4.8$ vs. $16.2 \pm 1.5\,\text{Mg C ha}^{-1}\,\text{yr}^{-1}$, respectively). This assumes near-equilibrium conditions, but at the Caxiuanã tower plot there is little evidence of the numerous large fallen trees seen at Tapajós km 67 (Y. Malhi, personal observations).

Belowground (BG) C stocks have rarely been measured by direct harvesting, except in the Manaus vicinity by Klinge (1973) and more recently by Higuchi (unpublished data). Estimates based on soil cores or pits tend to underestimate biomass by not including the core root areas immediately underneath trees. To estimate BG biomass in Table 1, we multiply the AG biomass values for the plateaux by a root:shoot ratio of $0.21 \pm 0.03$, encompassing the values reported for the tropics in the global surveys of Jackson *et al.* (1996) and Cairns *et al.* (1997). A similar value of 0.21 has been confirmed by extensive and comprehensive BG biomass sampling of 131 trees in the vicinity of the Bionte plots near Manaus (N. Higuchi *et al.*, unpublished data).

Soil C stocks are usually reported only for the top 30 cm or top 1 m of soil, and range between 74 and 127 Mg C ha$^{-1}$ yr$^{-1}$. Quesada *et al.* (2008) report C stocks for all three sites to 2 m depth, showing substantial C stocks at these depths and evidence for further C storage at greater depths, particularly at Tapajós.

Total C stocks to 2 m depth are presented in Fig. 2. For soil C stocks, we employ values reported by Quesada *et al.* (2008), as they have applied the same sampling methodologies and lab analyses at all three sites and are thus comparable across sites (see the Supporting information). Total AG C stocks are similar at all three sites (Manaus 199 Mg C ha$^{-1}$, Tapajós 202 Mg C ha$^{-1}$, Caxiuanã 231 Mg C ha$^{-1}$), with the smaller amount of biomass in living vegetation at Tapajós compensated for by the higher CWD. BG C stocks to 2 m depth are very similar in magnitude to AG stocks, with Tapajós showing the highest soil C stocks. Total C stocks are 403 Mg C ha$^{-1}$ Manaus, 416 Mg C ha$^{-1}$ Tapajós, 423 Mg C ha$^{-1}$ Caxiuanã. These values would certainly increase if greater soil depths are considered, and would be much lower for Manaus if the full plateau–valley landscape were considered.

### Leaf area index (LAI) and nutrient status (Tables 2 and 3)

The LAI is an important physiological property, and will be important later in our paper when we attempt to scale leaf respiration rates. The LAI of each site is tabulated in Table 2, and leaf nutrient properties are listed in Table 3. Nutrient status was determined by Patiño *et al.* (in review) by collection of leaves at various heights for 19–30 individuals in each plot (Supporting information). The values reported here are simply the means for each plot, with no attempt at weighted scaling. Features that stand out are the much higher leaf calcium (Ca) status at Tapajós (twice as high as Manaus or Caxiuanã), and the significantly higher leaf phosphorus (P) status. These differences are found across the population and not driven by a few outlier samples. The higher mean leaf aluminium (Al) content at Tapajós is driven by seven individuals having very high Al content, whereas leaves at Caxiuanã appear to have significantly lower potassium (K) content.

### Soil chemical and physical properties (Table 4)

Soil samples for all three sites have been collected by Quesada *et al.* (2008) and analysed to a common protocol (see the Supporting information). Properties for soil depths 0–30 cm are summarised in Table 4. These highly weathered soils (predominantly ferralsols/oxisols on the plateau) generally have low cation exchange capacity, low pH and high Al content. For P, readily available P is defined as sum of the P immediately accessible in solution (measured as the resin P), plus that organic and inorganic P which can be extracted by sodium bicarbonate. This appears a good measure of the weakly bound P that plant roots are able to extract at little cost, and hence a good measure of plant P availability (Quesada *et al.*, 2008). As with the leaves, soil P and Ca concentrations seem much higher at Tapajós (although still low). The Belterra clay soils of Tapajós have very high clay content (90%) while the other

**Table 1** Carbon stocks for each site, in $MgC\,ha^{-1}$

| Stock | Site | Subsite | Carbon stock | Reference |
|---|---|---|---|---|
| AG biomass | Manaus | Bionte (3 ha) | $180 \pm 10$ | Higuchi, unpublished data |
| | | Jacaranda (10 ha) | 148 | Malhi et al. (2006) |
| | | BDFFP (26 ha) | $165 \pm 5$ | Malhi et al. (2006) |
| | | BDFFP (20 ha) | $167 \pm 3$ | Pyle et al. (2008) |
| | Tapajós | km 67 (20 ha) | $143.7 \pm 5.4$ | Rice et al. (2004) |
| | | km 67 (20 ha) | $148 \pm 3$ | Pyle et al. (2008) |
| | | km 72 (10 ha) | $150 \pm 4$ | Pyle et al. (2008) |
| | | km 117 (20 ha) | $147 \pm 5$ | Pyle et al. (2008) |
| | | km 117 (3 ha) | $175 \pm 12$ | Malhi et al. (2006) |
| | Caxiuanã | Tower plot (1 ha) | 209 | S. Almeida, unpublished data |
| | | CAX-01, 02 (2 ha) | 191 | S. Almeida, unpublished data |
| | | TEAM 01-06 (6 ha) | $203 \pm 9$ | S. Almeida, unpublished data |
| Coarse woody debris | Manaus | Jacaranda | 10.5 | Chambers et al. (2000) |
| | Manaus | BDFFP | $16.2 \pm 1.5$ | Pyle et al. (2008) |
| | Tapajós | km 67 tower | $48 \pm 5.2$ | Rice et al. (2004) |
| | | km 67 | $43.9 \pm 5.2$ | Pyle et al. (2008) |
| | | km 72 | $41.0 \pm 6.3$ | Pyle et al. (2008) |
| | | km 117 | $43.0 \pm 12.1$ | Pyle et al. (2008) |
| | Caxiuanã | All plots | $15.3 \pm 4.8$ | Estimated, this study* |
| Forest floor | Manaus | Near km 34 tower | $3.0 \pm 0.6$ | Luizao et al. (2004) |
| | | Jacaranda transects | $4.0 \pm 0.9$ | Chambers et al. (2004) |
| | Tapajós | Near km 67 tower | $3.10 \pm 0.47$ clay | Silver et al. (2000) |
| | | | $4.39 \pm 0.47$ sand | |
| | Caxiuanã | Near flux tower | $2.0 \pm 2.0$ | Metcalfe et al. (2007) |
| BG biomass (0–1 m) | Manaus | Bionte | $38 \pm 6$ | Estimated, this study† |
| | Caxiuanã | Tower plot | $44 \pm 7$ | Estimated, this study† |
| | Tapajós | km 67 tower | $30 \pm 4$ | Estimated, this study† |
| Soil C (0–1 m) | Manaus | km 34 | 127 | Quesada et al. (2008) |
| | Tapajós | km 67 tower | 120 | Quesada et al. (2008) |
| | | Near km 67 tower | $80 \pm 3$ clay | Silver et al. (2000) |
| | | | $81 \pm 4$ sand | |
| | Caxiuanã | | 98 clay | Ruivo and Cunha (2003) |
| | | | 90 sand | |
| | | Tower plot | 105 | Quesada et al. (2008) |
| | | Plot CAX-01 | 84 | Quesada et al. (2008) |
| | | Plot CAX-02 | 68 | Quesada et al. (2008) |
| | | Drought plot | 74 | Quesada et al. (2008) |
| Soil C (1–2 m) | Manaus | km 34 plateau | 38 | Quesada et al. (2008) |
| | | km 34 valley | | Quesada et al. (2008) |
| | Tapajós | km 67 tower | 63 | Quesada et al. (2008) |
| | Caxiuanã | Tower plot | 43 | Quesada et al. (2008) |
| | | Plot CAX-01 | 35 | Quesada et al. (2008) |
| | | Plot CAX-02 | 30 | Quesada et al. (2008) |
| | | Drought plot | 28 | Quesada et al. (2008) |
| Soil C (2–3 m) | Tapajós | km 67 tower plot | 37 | Quesada et al. (2008) |
| | Caxiuanã | Drought plot | 19 | Quesada et al. (2008) |

*CWD stocks at Caxiuanã are estimated by dividing the measured biomass mortality rate in the period 2003–2006 ($2.44 \pm 0.47\,MgC\,ha^{-1}\,yr^{-1}$) by a decay constant $k_{wood}$ of $0.16 \pm 0.04\,year^{-1}$, with error bars encompassing the values reported later in this paper for other sites.

†BG biomass at selected sites is estimated by multiplying the AG biomass by a root:shoot ratio of $0.21 \pm 0.03$. See main text for references.

AG, aboveground; BG, belowground; BDFFP, Biological Dynamics of Forest Fragments Project; CWD, coarse woody debris.
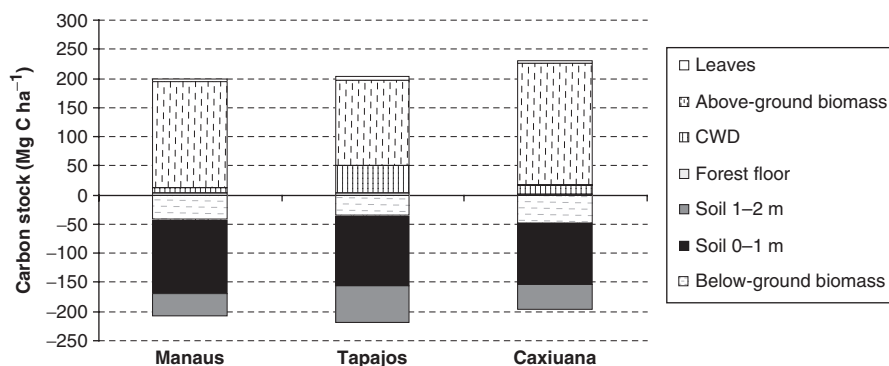
**Fig. 2** Component and total carbon (C) stocks at each site, to 2 m depth, in Mg C ha$^{-1}$. Belowground C stocks are assigned negative values.

**Table 2** Measurements of leaf area index (LAI) at each site

| Site | Subsite | Method | Value | Reference |
|------|---------|--------|-------|-----------|
| Manaus | k34 | Hemiphoto | $5.6 \pm 0.2$ | Patiño *et al.* (in review) |
| | Ducke | Destructive harvest (400 m$^2$) | $5.7 \pm 0.5$ | McWilliam *et al.* (1993) |
| | Jacaranda | Allometric relation | 4.7 | Chambers *et al.* (2004) |
| Tapajós | km 67 | Hemiphoto | $6.4 \pm 0.1$ | Patiño *et al.* (in review). |
| | Near km 67 | LAI 2000 | $5.1 \pm 0.4$ | Aragão *et al.* (2005) |
| | Near km 67 | | 4.5 | Domingues *et al.* (2005) |
| Caxiuanã | Tower plot | Hemiphoto | $5.3 \pm 0.1$ | Patiño *et al.* (in review) |
| | CAX-01 | Hemiphoto | $5.9 \pm 0.2$ | Patiño *et al.* (in review) |
| | CAX-02 | Hemiphoto | $5.7 \pm 0.1$ | Patiño *et al.* (in review) |

**Table 3** Leaf nutrient properties at each site

| | Site | Manaus | Tapajós | Caxiuanã |
|---|------|--------|---------|----------|
| | *n* | 19 | 33 | 19 |
| LMA | g m$^{-2}$ | 103 + 6 | 96 + 5 | 90 + 7 |
| N | mg g$^{-1}$ | 23.1 + 1.3 | 22.9 + 1.3 | 19.8 + 1.2 |
| C | % | 50.0 + 0.6 | 48.0 + 0.7 | 48.0 + 0.7 |
| Al | mg g$^{-1}$ | 0.32 + 0.15 | 2.75 + 1.08 | 0.21 + 0.03 |
| Ca | mg g$^{-1}$ | 3.06 + 0.46 | 7.93 + 0.74 | 3.87 + 0.59 |
| K | mg g$^{-1}$ | 4.03 + 0.45 | 3.58 + 0.35 | 1.95 + 0.23 |
| Mg | mg g$^{-1}$ | 2.12 + 0.24 | 2.56 + 0.23 | 2.24 + 0.28 |
| P | mg g$^{-1}$ | 0.64 + 0.04 | 0.75 + 0.04 | 0.60 + 0.04 |

plateau soils are more clay–loam in texture, and the valley-bottom spodosols in the Manaus landscape are sandy. Most of the readily available nutrients are associated with clay surfaces, and the readily available P per unit of clay is relatively constant across all three plateau sites (but not in the sandy valley bottoms).

### Aboveground net primary productivity (AGNPP)

*Aboveground stem productivity (Table 5).* Wood productivity is the most visible aspect of forest productivity, and can be measured by recensus of tree diameters and new recruits. The basic measurement can be adjusted by correction for census interval (Malhi *et al.*, 2004) and species- or genus-specific wood density (discussed in the Supporting information).

There is little variation in stem productivity between the Manaus and Caxiuanã plots, ranging between 2.0 and 2.9 Mg C ha$^{-1}$ yr$^{-1}$ for all sites but one, values that are typical of eastern Amazonian forests as reported by Malhi *et al.* (2004). Tapajós tends to show higher wood productivity over a wide area, particularly in the larger-scale censuses (Pyle *et al.*, 2008). This appears to be correlated with the high CWD, indicating a large-scale disturbance event in the Tapajós region in recent years.

For the synthesis table, we distil the following values. For Manaus, we average the values from the Bionte, Jacaranda and BDF plots (using the recent values from Pyle *et al.* 2008), 33 ha in total. For Tapajós, we average the two surveys at km 67 reported by Pyle *et al.* (20 ha in total). For Caxiuanã, we average values from Cax-01 and Cax-02, the tower plot, and the six TEAM plots (9 ha in total). All averages are weighted by plot size and the square root of total census period. The resulting values are reported in Table 13.

**Table 4** Soil chemical and physical properties

| Site and subsite | Units | Manaus Jacaranda | | Tapajós km 67 tower | Caxiuanã tower plot |
|---|---|---|---|---|---|
| | | Valley | Plateau | | |
| Soil type | | Umbric podzol | Geric ferralsol | Geric ferralsol | Geric acric ferralsol |
| Clay mineralogy | | Quartz | Nacrite | Nacrite | Kaolinite |
| pH (in water, 1 : 2.5) | | 4.73 | 3.94 | 3.84 | 3.79 |
| Resin P | mg kg$^{-1}$ | 0.97 | 1.94 | 7.63 | 2.34 |
| Readily available P | mg kg$^{-1}$ | 9.21 | 12.92 | 20.08 | 12.31* |
| N (%) | % | 0.08 | 0.15 | 0.17 | 0.13 |
| C (%) | % | 1.34 | 2.59 | 2.54 | 1.68 |
| C/N ratio | | 16.96 | 16.79 | 15.16 | 13.09 |
| Ca | cmol kg$^{-1}$ | 0.025 | 0.111 | 0.303 | 0.129 |
| Mg | cmol kg$^{-1}$ | 0.055 | 0.101 | 0.225 | 0.147 |
| K | cmol kg$^{-1}$ | 0.041 | 0.095 | 0.073 | 0.048 |
| Na | cmol kg$^{-1}$ | 0.013 | 0.063 | 0.040 | 0.083 |
| Al | cmol kg$^{-1}$ | 0.18 | 1.82 | 2.33 | 1.88 |
| Sum of bases | cmol kg$^{-1}$ | 0.13 | 0.37 | 0.64 | 0.41 |
| Exchangeable CEC | cmol kg$^{-1}$ | 0.31 | 2.19 | 2.97 | 2.28 |
| Al saturation | cmol kg$^{-1}$ | 57.27 | 83.16 | 78.45 | 82.20 |
| Porosity | % | 42.73 | 16.84 | 21.55 | 17.80 |
| Sand fraction | % | 95.76 | 20.97 | 2.86 | 32.54 |
| Clay fraction | % | 1.84 | 66.21 | 89.25 | 53.76 |
| Silt fraction | % | 2.40 | 12.81 | 7.89 | 13.70 |

*The measurement of readily available phosphorus at Caxiuanã is from plots CAX-01 and CAX-02, not from the tower plot.

**Table 5** Aboveground wood production estimates (Mg C ha$^{-1}$ yr$^{-1}$)

| Site | Subsite | Years | Wood productivity | Author |
|---|---|---|---|---|
| Manaus | Jacaranda, (10 ha) | | 2.8 | Chambers *et al.* (2004) |
| | Jacaranda (10 ha) | 1996–2002 | 2.11 ± 0.10 | Malhi *et al.* (2004) |
| | Bionte (3 × 1 ha) | 1986–2006 | 2.45 ± 0.06 | Higuchi *et al.* (unpublished, updated from Malhi *et al.* (2004) |
| | BDFFP (12 × 1 ha) | 1981–1999 | 2.11 ± 0.07 | Malhi *et al.* (2004) |
| | BDFFP (20 ha) | 1997/8–2002/4 | 2.84 ± 0.10 | Pyle *et al.* (2008) |
| Caxiuanã | Clay/sand (Cax-01 and Cax-02) (2 ha) | 1994–2003 | 2.53 ± 0.40 | Almeida unpublished data, updated from Malhi *et al.* (2004) |
| | Tower plot (clay) (1 ha) | 2004–2006 | 2.49 ± 0.32 | Almeida, unpublished data |
| | TEAM plots 1–6 (6 × 1 ha) | 2003–2006 | 2.02 ± 0.20 | Almeida, unpublished data |
| Tapajós | km 67 (4 ha) | 1999–2001 | 3.81 ± 0.22 | Rice *et al.* (2004) |
| | km 67 (20 ha) | 1999–2005 | 3.76 ± 0.07 | Pyle *et al.* (2008) |
| | km 72 (10 ha) | 2003–2005 | 4.33 ± 0.17 | Pyle *et al.* (2008) |
| | km 117 (20 ha) | 2003–2005 | 3.20 ± 0.12 | Pyle *et al.* (2008) |
| | km 117 (3 ha) | 1983–1995 | 2.60 ± 0.07 | Malhi *et al.* (2004) |
| | Drought control (1 ha) | 1999–2000 | 2.78 | Nepstad *et al.* (2002) |
| | Drought treatment plot (predrought) (1 ha) | 1999 | 2.85 | Nepstad *et al.* (2002) |

BDFFP, Biological Dynamics of Forest Fragments Project.

*Fine litterfall (Table 6).* Fine litter includes leaves, twigs (typically <1 cm diameter), flowers and fruit, and is measured through an array of litter traps collected at frequent (e.g. biweekly) intervals to minimise decomposition (Clark *et al.*, 2001a). Productivity estimates based on litterfall rely on the assumption that the litterfall is approximately equal to productivity of that component. This assumption is weaker if interannual variability is significant, especially for larger components such as branches, and is also complicated by the trapping and *in situ* decomposition of dead material in the canopy , and by

**Table 6** Fine litterfall estimates (MgC ha$^{-1}$ yr$^{-1}$)

| Site | Subsite | Years | Litterfall rate | Author |
|------|---------|-------|-----------------|--------|
| Manaus | Jacaranda | | 3.3 | Chambers *et al.* (2004) |
| | | 2000–2001 | 4.0 ± 0.6 plateau | Luizao *et al.* (2004) |
| | | | 3.6 ± 0.2 slope | |
| | | | 3.1 ± 0.4 valley | |
| Caxiuanã | Drought control | 2001–2004 | 3.7 | S. Almeida unpublished data |
| | Tower plot | 2005–2006 | 3.84 ± 0.32 | S. Almeida, unpublished data |
| Tapajós | km 67 | 1999–2001 | 6.025 | Rice *et al.* (2004) |
| | Near km 67 | July 1999–May 2001 | 6.93 ± 0.82 clay soil | Silver *et al.* (2005) |
| | | | 7.27 ± 0.98 sand soil | |
| | Drought control | 2000–2005 | 3.3 ± 0.1 | Brando *et al.* (2008) |
| | Drought treatment | 2000 | 4.8 ± 0.6 | Nepstad *et al.* (2004) |

**Table 7** Carbon flows through tree mortality (MgC ha$^{-1}$ yr$^{-1}$)

| Site | Subsite | Years | Mortality | Author |
|------|---------|-------|-----------|--------|
| Manaus | Bionte 3 × 1 ha | 1986–2006 | 1.62 ± 0.17 | Higuchi *et al.* (unpublished data) |
| | BDFFP | 1997/8–2002/4 | 2.58 ± 0.16 | Pyle *et al.* (2008) |
| Caxiuanã | Clay/sand (Cax-01 and Cax-02) | 1994–2003 | 1.43 ± 0.44 | S. Almeida unpublished data, updated from Malhi *et al.* (2004) |
| | Tower plot (clay) | 2004–2006 | 2.04 ± 0.56 | Almeida, unpublished data |
| | TEAM plots 1–6 | 2003–2006 | 2.14 ± 0.45 | Almeida, unpublished data |
| Tapajós | km 67 (20 ha) | 1999–2005 | 2.74 ± 0.17 | Pyle *et al.* (2008) |
| | km 72 (10 ha) | 2003–2005 | 2.39 ± 0.35 | Pyle *et al.* (2008) |
| | km 117 (20 ha) | 2003–2005 | 2.41 ± 0.29 | Pyle *et al.* (2008) |

herbivory. Details of litterfall collection methods at each site are given in the Supporting information.

Fine litterfall values range for most sites between 3.3 and 4.8 MgC ha$^{-1}$ yr$^{-1}$. The tower plot at Tapajós km 67 is again an exception, with Rice *et al.* (2004) reporting 6.0 MgC ha$^{-1}$ yr$^{-1}$ and Silver *et al.* (2000) reporting $\sim$ 7.1 MgC ha$^{-1}$ yr$^{-1}$; however, the nearby drought experiment shows values similar to other sites. The ratio between fine litterfall and coarse wood production at Tapajós km 67 is similar to the other sites. At Caxiuanã, 73% of the litter was from leaves, 12% from flowers and fruit, 8% twigs, and 7% unidentifiable (S. Almeida and L. Aragão, unpublished data).

For the synthesis table (Table 13), we distil the following values. For Manaus, a mean of the Luizão *et al.* (2004) values; Chambers *et al.*, 2004 comment that the landscape is approximately equally divided between plateau, slopes and valleys; for Caxiuanã, the tower plot values (the drought control is more sandy), for Tapajós a weighted average of the Rice *et al.* (2004) and Silver *et al.* (2000) values from the km 67 tower plot, and the 6-year dataset from the drought control plots.

*Coarse woody litterfall (Table 7).* Woody litterfall can be an important component of forest productivity, but is

challenging to measure. It can be divided into three components: trunk mortality, massive branch shedding, and twig and small branch fall (pieces between 1 and 10 cm diameter). The division from fine litterfall is often set at 1 cm diameter for twigs. This division is largely for methodological convenience; small branches are too heterogeneous in placement and too large to be adequately captured by fine litter traps.

Trunk mortality should be close to wood productivity for quasi-equilibrium forests, although for many plots it has been reported to be slightly lower, resulting in a slight net AG biomass increment over time. It can be measured directly and these values are reported in Table 7, and will be used later for estimation of soil respiration. As with productivity estimates, these values incorporate species-specific wood density for all except the Pyle *et al.* (2008) estimates at Tapajós and BDFFP. For the synthesis table (Table 13), we distil the following values. For Manaus, we average the Bionte and BDFFP values; for Tapajós, we average the two surveys at km 67 reported by Pyle *et al.* (20 ha in total); and for Caxiuanã, we average the values reported from all nine 1 ha plots. All averages are weighted by plot area and by the square root of the duration of each study plot.

**Table 8** Coarse woody litterfall estimates ($MgC ha^{-1} yr^{-1}$)

| Site | Subsite | Years | Branchfall rate | Author |
|------|---------|-------|-----------------|--------|
| Manaus | Jacaranda | | 0.4 | Chambers *et al.* (2001a) |
| Tapajós | Drought control | 1999–2000 | $1.8 \pm 0.8$ | Nepstad *et al.* (2004) |
| | Drought control | 2002–2006 | $1.6 \pm 0.8$ | Brando *et al.*, unpublished data |
| | Drought treatment | 1999 | $1.55 \pm 0.8$ | Nepstad *et al.* (2004) |

Massive branch loss (Table 8) was surveyed for Manaus by Chambers *et al.* (2001a) and reported to be $0.4 MgC ha^{-1} yr^{-1}$. Nepstad *et al.* (2002) and P. Brando *et al.* (unpublished data) measured branch shedding at the Tapajós drought experiment by conducting frequent surveys of three $1 m \times 100 m$ transects in each plot (drought control and treatment), and report longterm branchfall rates of $1.6 \pm 0.8 MgC ha^{-1} yr^{-1}$ for the drought control plot. Hence, we estimate that branch loss averages $\sim 1 MgC ha^{-1} yr^{-1}$, with a conservative uncertainty of $\pm 100\%$ (Table 13).

*Volatile organic compound (VOC) production.* The emission of VOCs from vegetation is a source of C from the vegetation, and can play an important role in local and regional atmospheric chemistry. For the K34 tower near Manaus, Kuhn *et al.* (2007) report a total 24 h VOC flux (isoprene plus monoterpenes) of $24 mgC m^{-2} day^{-1}$ for the period 17–25 July 2001, which if fairly invariant over the year is equivalent to an annual total of $0.088 Mg C ha^{-1} yr^{-1}$. Similar values were reported by Greenberg *et al.* (2004) at Tapajós and by previous studies north of Manaus [summarised in Kuhn *et al.* (2007)]. In C terms alone, the VOC flux is clearly a small component of the internal C cycle, and for our synthesis table we allocate a value of $0.1 \pm 0.05 MgC ha^{-1} yr^{-1}$ for all sites.

Methane emissions from upland tropical forests are a new subject of interest, but still controversial. Do Carmo *et al.* (2006) applied a canopy budget model to measured soil–atmosphere fluxes of methane to estimate net methane emissions from upland forests of $2–21 mg CH_4 m^{-2} day^{-1}$, equivalent to $0.005–0.06 MgC ha^{-1} yr^{-1}$. Taking the midrange, we allocate $0.03 \pm 0.03 MgC ha^{-1} yr^{-1}$ to methane emissions. Combining these with our estimate of isoprene and monoterpene emissions, we arrive at an estimate of total volatile emissions of $0.13 \pm 0.06 MgC ha^{-1} yr^{-1}$ (Table 13).

*Belowground net primary productivity (BGNPP)*

*Fine root productivity (Table 9).* Fine root productivity is defined as the production of root material less than a threshold diameter, usually 2 mm. The value calculated for fine root production can depend on sampling methodology, in particular, the technique employed and the depth to which the soil is sampled.

Fine root production values have been reported for Caxiuanã and Tapajós (Silver *et al.*, 2005; Metcalfe *et al.*, 2008; Table 9). Details of the measurements and correction procedures are discussed in Supporting information. An important discrepancy between these two studies is the depth to which root production is measured, 30 cm at Caxiuanã vs. 10 cm at Tapajós. We attempt to standardise fine root productivity estimates by applying a depth-scaling factor to each study (discussed in the Supporting information). For Caxiuanã, this correction factor (30–100 cm) is $1.3 \pm 0.1$, for Tapajós (10–100 cm) it is $2.1 \pm 0.4$. Application of this depth correction greatly reduces the difference between the two studies (Table 9).

For the synthesis table (Table 13), we distil the values multiplied to 1.0 m depth. For Caxiuanã, the tower plot values are used (the drought control is more sandy). For Tapajós, the values are weighted according to the proportion of sand and clay in the plot (32% and 68%, respectively). For Manaus, no data were available and we take the mean of the Caxiuanã and Tapajós values, with conservative error bars of $\pm 1.0 MgC ha^{-1} yr^{-1}$.

*Coarse root productivity.* Coarse root productivity is the productivity of larger, more lignified roots. These can be divided into roots $<10 cm$ diameter, which can be expected to be reasonably homogeneous in distribution and amenable to conventional random or grid-based sampling, and massive structural roots which are very difficult to assess for biomass without excavation, and even more difficult to monitor over time.

Metcalfe *et al.* (2008) used a coring approach to estimate the coarse root productivity of small and medium roots at Caxiuanã to be $4 MgC ha^{-1} yr^{-1}$. For massive structural roots, the best approach may be to assume that wood production per unit biomass is the same as for AG woody biomass, and use the estimate of BG biomass being $21 \pm 3\%$ of AG biomass (see 'C stocks'). This yields values of $2.9 \pm 0.6 MgC ha^{-1} yr^{-1}$ (Caxiuanã), $2.8 \pm 0.7 MgC ha^{-1} yr^{-1}$ (Manaus) and $3.0 \pm 0.5 MgC ha^{-1} yr^{-1}$ (Tapajós); these are the values distilled in Table 13.

*Dissolved organic C deposition and leakage.* Waterloo *et al.* (2006) measured dissolved organic carbon (DOC) runoff in the Igarapé Açu catchment (2°36′S, 60°12′W), which

**Table 9** Fine root productivity estimates (in $MgC\,ha^{-1}\,yr^{-1}$) with a correction to 1.0 m depth

| Site | Subsite | Years | Fine root production | Corrected to 1.0 m | Author |
|------|---------|-------|----------------------|--------------------|--------|
| Caxiuanã | Clay soil | 2004–2005 | 1.67 ± 0.41* | 2.16 ± 0.55 | Metcalfe *et al.* (2008) |
| | Sand soil | 2004–2005 | 1.85 ± 0.45* | 2.40 ± 0.61 | Metcalfe *et al.* (2007b) |
| Tapajós | km 67, clay | | 0.91 ± 0.08† | 1.9 ± 0.4 | Silver *et al.* (2000) |
| | km 67, sand | | 1.06 ± 0.23† | 2.2 ± 0.6 | Silver *et al.* (2000) |

*Includes depth correction and measured C content ($\sim 0.45$).
†0–10 cm depth, and assuming C = 0.5.

covers an area of $6.8\,km^2$, including the Manaus K34 micrometeorological tower. Surface runoff dominated the water flow out of the catchment ($1362\,mm\,yr^{-1}$ in 2002 and $780\,mm\,yr^{-1}$ in 2003, and groundwater flow was negligible ($0.8\,mm\,yr^{-1}$). Organic C exports were dominated by dissolved organic C, with exports in sediment constituting 6–8% of the total. Net C exports amounted to 0.262 and $0.117\,MgC\,ha^{-1}\,yr^{-1}$ in 2002 and 2003, respectively, with the 2-year mean being $0.19 \pm 0.07\,MgC\,ha^{-1}\,yr^{-1}$ (error bars encompass the two annual values). Almost all of this export seemed to originate in the riparian zone of the valley bottoms (per unit area export rates of $0.31–0.71\,MgC\,ha^{-1}\,yr^{-1}$), which cover 35% of the watershed area. For plateau regions, the total DOC exports through groundwater seemed to be less than $0.0005\,MgC\,ha^{-1}\,yr^{-1}$. The figures for the Açu catchment are comparable with the annual average C export for the Rio Negro basin over 1982–1984 of $0.126\,MgC\,ha^{-1}\,yr^{-1}$ (Richey *et al.*, 1990).

Waterloo *et al.* (2006) measured DOC concentrations in rainfall of $1.2\,mg\,L^{-1}$, thus estimating annual DOC deposition rates in dissolved rainwater of 0.035 and $0.024\,MgC\,ha^{-1}\,yr^{-1}$. A significant proportion of DOC inputs are probably derived from scavenging of aerosols during rainfall formation, and dry deposition on the rain gauge.

For our synthesis table, for Caxiuanã and Manaus, we use directly the values reported by Waterloo *et al.* (2006). The Tapajós site is a plateau cut by few rivers, so we employ the values for only plateaux reported by Waterloo *et al.* We report net DOC export (DOC runoff−DOC deposition). In all cases, DOC transfer is clearly a very small component of the forest C cycle.

### Dead material dynamics

The dynamics of fine litter are reasonably straightforward, as most of it turns over on timescales $\sim 1$ year (range: 6 months to 2 years), that is, the decay constant $k_{litter} \sim 1$ year$^{-1}$ (range: 0.5–2.0 year$^{-1}$). The mean annual stock of surface fine litter is approximately $NPP_l/k_{litter}$, but shows substantial seasonal variability with a peak in the dry season (a time of high litterfall and slow, moisture-limited, decay rate). Dividing the reported values litterfall rates by $k_{litter} = 1.0 \pm 0.5$ year$^{-1}$, we estimate mean annual fine litter stocks of $3.6 \pm 1.9\,MgC\,ha^{-1}$ (Manaus), $6.5 \pm 3.3\,MgC\,ha^{-1}$ (Tapajós) and $3.8 \pm 1.9\,MgC\,ha^{-1}$ (Caxiuanã). The C stock of the fine litter layer has been estimated at the Manaus transect plots to be $4.0 \pm 0.9\,MgC\,ha^{-1}$, and at Caxiuanã to be $1.9 \pm 2.5\,MgC\,ha^{-1}$ (clay) and $2.1 \pm 1.6\,MgC\,ha^{-1}$ (sand; Metcalfe *et al.*, 2007), of similar magnitude to our estimates, but these measurements may be subject to seasonal sampling bias.

The decomposition of CWD is important on time scales of 5–10 years, that is, the decay constant $k_{CWD} \sim 0.1–0.2$ year$^{-1}$ (Chambers *et al.*, 2000; Keller *et al.*, 2004). As with fine litter, the equilibrium CWD stock is $\sim$ (trunk mortality and branch shedding)/$k_{CWD}$, but the CWD stock can increase greatly in the wake of episodes of greater mortality. At Manaus, Chambers *et al.* (2000) estimated $k_{CWD} \sim 0.19$ over a 10–15 year period. At Tapajós km 67, Keller *et al.* (2004) estimated a value of $k_{wood}$ of 0.124, whereas Baker *et al.* (2007) suggested $k_{CWD} \sim 0.2$ for sites in southern Peru, where mean wood densities are lower and nutrient content higher.

Respiration from CWD is a component of ecosystem heterotrophic respiration that is largely missed by measurement of soil respiration. An important parameter is the fraction of CWD that is respired *in situ*, rather than being transferred to the soil C pool, either by transport by soil fauna or when the CWD is sufficiently decomposed to not be readily distinguishable from soil material. This transfer parameter can be estimated (under equilibrium conditions) as the ratio of the CWD respiratory efflux to the CWD influx. At the Manaus transect site, Chambers *et al.* (2001b) estimated that respiration rates from coarse surface litter were $\sim 1.9 \pm 0.2\,MgC\,ha^{-1}\,yr^{-1}$, declining sharply when moisture content fell. In total, Chambers *et al.*, estimated that 76% of the mass loss of CWD was by wood respiration, with 24% of the CWD C implicitly being transported to the soil C pool. Chambers *et al.* do not

report errors bars for this fraction; we assign a plausible estimate of $76 \pm 15\%$. In Tapajós, Hutyra *et al.* (2008) estimated much larger wood respiration rates of $4.5 \pm 1.1\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$, consistent with the high CWD stocks that indicate that this is a postdisturbance forest. Coarse woody respiration rates can also be estimated from the mortality inputs (stem mortality plus branch loss, multiplied by $0.76 \pm 0.15$ according to Chambers' estimate). This approach gives $2.55 \pm 0.51\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ for Manaus, $2.84 \pm 0.57\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ for Tapajós and $2.19 \pm 0.49\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ for Caxiuanã. The fact that this estimated value at Tapajós is lower than that observed (Hutyra *et al.*, 2008) again reflects the nonequilibrium status of the CWD stocks at that site. For the synthesis table (Table 13), we employ these equilibrium estimates for Manaus and Caxiuanã, and the directly observed values for Tapajós. The equilibrium value for Manaus is favoured over Chambers' direct measurement as it incorporates a much more extensive mortality dataset.

### Respiration rates

*Soil respiration (Table 10).* Soil respiration is one of the most reported measurements of internal C dynamics (Table 10). Despite the range of methods used (static chambers, dynamic flow chambers), the reported annual soil respiration values at each site are remarkably consistent, in the range $10–15\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$, with the notable exception of Sotta *et al.* (2004) for Manaus, which suggests a systematic overestimation in that study. For the synthesis table (Table 13), at Manaus we average the values reported by Chambers *et al.* (2004), at Caxiuanã we take the values from the tower plot, and at Tapajós we average the various reported values, first weighting by soil type for the Silver *et al.* (2000) data. Error estimates

are not given for Manaus and we apply those estimated for Tapajós.

*Root respiration (Table 11).* The partitioning of soil respiration into autotrophic and heterotrophic respirations, and thereafter into values per unit biomass, is helpful in terms of interpreting processes, but presents numerous methodological challenges (Baggs 2006). Partitioning of soil respiration has been attempted at Caxiuanã (Metcalfe *et al.*, 2007) and Tapajós (Silver *et al.*, 2005), using very different methodologies (see the Supporting information).

There is a factor of two difference between the Silver *et al.*, and Metcalfe *et al.* estimates. This could reflect (i) genuine between-site differences, (ii) an overestimation of root respiration by the extraction method employed at Caxiuanã, and (iii) an overestimation of heterotrophic respiration by the trenching and mass balance approaches used at Tapajós.

For the synthesis table (Table 13), for Caxiuanã we employ values for the clay soil only, and for Tapajós we take a mean weighted by the relative distribution of sand and clay soils (32 : 68%). For Manaus, we have no direct data and take the mean of the Caxiuanã and Tapajós values, with conservative error bars of $\pm 2\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ to encompass the mean values of both other sites.

*Stem respiration.* The efflux of $CO_2$ from stem is the product of metabolic activity associated with woody stem growth and maintenance, plus possibly some additional dissolved $CO_2$ carried in the transpiration stream. Stem respiration has been measured at all three sites (see the Supporting information for further details). The usual approach (e.g. Chambers *et al.*, 2004) is to measure a number of trees at approximately 1.3 m height, employ allometric equations relating tree diameter to total tree surface area, and scale up to the plot

**Table 10** Measured soil respiration rates (in $\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$)

| Site | Subsite | Years | Soil respiration | Author |
|---|---|---|---|---|
| Manaus | Jacaranda | 07/2000–06/2001 | 14.4 plateau<br>12.1 slope<br>9.8 valley<br>12.1 mean | Chambers *et al.* (2004) |
| | C14 | 05/1997-12/1997 | 25.7 plateau | Sotta *et al.* (2004) |
| Caxiuanã | Clay | 11/2004-11/2005 | 12.8 (10.18) | Metcalfe *et al.* (2007) |
| | Clay | 12/2001-11/2003 | 11.66 ± 0.26 | Sotta *et al.* (2006) |
| | Sand | | 13.2 (9.20) | Metcalfe *et al.* (2007) |
| | Sand | 12/2001-11/2003 | 14.89 ± 0.23 | Sotta *et al.* (2006) |
| Tapajós | Near km 67 clay | 07/1999-05/2001 | 10.84 ± 0.5 | Silver *et al.* (2005) |
| | Near km 67 sand | | 13.63 ± 2.09 | Silver *et al.* (2005) |
| | Drought control | 2000–2005 | 12.8 ± 0.7 | E. Davidson, unpublished data, updated from Davidson *et al.* (2004) |
| | km 67 | | 9.95 | Varner *et al.*, cited in Hutyra *et al.* (2007) |
| | km 67 | | 10.4 ± 0.2 | Keller *et al.* (2005) |

**Table 11** Measured root respiration rates (in $MgCha^{-1}yr^{-1}$)

| Site | Subsite | Years | Root respiration | Author |
|---|---|---|---|---|
| Caxiuanã | Clay | | 7.4 ± 0.5 | Metcalfe *et al.* (2007) |
| | Sand | | 5.8 ± 0.3 | Metcalfe *et al.* (2007) |
| Tapajós | Clay | | 3.0 ± 0.5 | Silver *et al.* (2000) |
| | Sand | | 5.2 ± 2.1 | Silver *et al.* (2000) |

by stratifying by either size class or growth class. Using this approach over a dry–wet seasonal cycle, Chambers *et al.* (2004) reported a mean annual stem respiration for the Manaus transect plots of $0.6\,\mu mol\,m^{-2}$ stem area $s^{-1}$, or $4.2\,MgCha^{-1}$ ground area $yr^{-1}$.

At the Tapajós drought experiment, Nepstad *et al.* (2002) also report a mean stem respiration rate of $0.62 \pm 0.08\,\mu mol\,m^{-2}$ stem area $s^{-1}$ from 21 nondroughted trees/lianas. Using the same surface area formula as Chambers *et al.* (2004), Hutyra *et al.* (2008) calculated the stem area index of the Tapajós plot as 1.55, giving a per unit ground area stem respiration of $1.0 \pm 0.12\,\mu mol\,m^{-2}\,s^{-1}$, or $3.8 \pm 1.0\,MgCha^{-1}yr^{-1}$.

At Caxiuanã, L. Teixeira *et al.* (unpublished data) report a mean stem respiration rate of $0.78 \pm 0.08\,\mu mol\,m^{-2}$ stem area $s^{-1}$ for 30 trees. The stem area index at the Caxiuanã tower plot was calculated to be 1.74, giving a per unit ground area stem respiration of $1.36 \pm 0.13\,\mu mol\,m^{-2}\,s^{-1}$, or $5.1 \pm 0.5\,MgCha^{-1}yr^{-1}$.

Similar values were reported by Meir & Grace (2002), with a mean value of $\sim 0.6\,\mu mol\,m^{-2}$ stem area $s^{-1}$ for 23 species at Jarú, Rondonia, Brazil. Yoda (1983) reported that stem respiration rates increase with height along the tree; hence, the branch respiration estimate of Chambers *et al.* (2004) is probably low. More recently, Cavaleri *et al.* (2008) reported that at La Selva, Costa Rica, per unit area respiration rates are much higher in branches than on the main trunk. This suggests that our estimates may be biased to being too low, although the total stem respiration reported at La Selva ($5.08 \pm 1.35\,MgCha^{-1}yr^{-1}$) is not very different form that reported at these Amazonian sites.

*Leaf respiration.* Respiration by leaves is a major plant metabolic activity, but is complicated by a number of definition and measurement issues. The first issue is to distinguish between photorespiration, the release of some $CO_2$ mediated by Rubisco and an intrinsic part of plant photosynthetic processes, and mitochondrial ('dark') respiration, which reflects the metabolic activity in the plant liberating energy utilised for plant maintenance and growth. In a diurnal cycle, mitochondrial respiration would be expected to increase

with leaf temperature (and the amplitude of the diurnal cycle varies considerably within the canopy according to leaf position and sun- and wind-exposure), but can also decrease strongly with increasing solar radiation (Atkin *et al.*, 2000). This decrease occurs because photosynthesis becomes a direct provider of adenosine triphosphate (ATP) for plant metabolic processes, reducing the demand for this from mitochondria.

The approach we adopt here is to attempt to estimate daytime photoinhibition, and hence arrive at a total leaf dark respiration term that incorporates all leaf mitochondrial activity. An alternative approach that is sometimes adopted (e.g. Litton *et al.*, 2007) is to focus only on night-time dark respiration (e.g. Lloyd *et al.*, 2002; Meir *et al.*, 2008), and incorporate daytime dark respiration into a net daytime C uptake term.

Widescale sampling of leaf dark respiration has been attempted at Manaus and Caxiuanã, and more limited sampling as been done at Tapajós. At Tapajós, Domingues *et al.* (2005) measured leaf dark respiration rates from light-response curves from 68 leaves from 26 individuals. Lloyd *et al.* (in press) took these values and applied the photoinhibition equations of Atkin *et al.* (2000) and integrated throughout the canopy. He calculated night-time leaf respiration of $5.6\,MgCha\,yr^{-1}$ and daytime leaf respiration of $1.8\,MgCha^{-1}yr^{-1}$ (a reduction of 67% in daytime dark respiration), giving a total leaf respiration of $7.4\,MgCha^{-1}yr^{-1}$. The applicability of the Atkin *et al.*, photoinhibition equation across a broad range of tropical species remains a large unknown, however.

For consistency, we apply a similar photoinhibition factor (67% of daytime leaf dark respiration, 34% of total leaf respiration) to Manaus and Caxiuanã, and use our hemiphoto-derived values of LAI for all sites. At Manaus (LAI $5.8 \pm 0.2$), Chambers *et al.* (2004) measured leaf respiration rates from leaves accessible *in situ* from canopy towers, (see the Supporting information for details). Our revised estimate of leaf respiration at Manaus is $10.0\,MgCha^{-1}yr^{-1}$, close to Chambers' original estimate of $9.8\,MgCha^{-1}yr^{-1}$.

At Caxiuanã (LAI $5.6 \pm 0.3$), leaf respiration rates have been measured from excised branches from 15 trees by Metcalfe *et al.* (submitted), and from 93 canopy trees by L. Aragão *et al.* (unpublished data). The measured mean respiration rates were $0.41 \pm 0.20\,\mu mol\,m^{-2}$ leaf area $s^{-1}$ (Metcalfe) and $0.84 \pm 0.09\,\mu mol\,m^{-2}$ leaf area $s^{-1}$ (Aragão). Averaging the two values and applying the same procedure as above (Supporting information), we estimate this gives a per ground area respiration of $8.9 \pm 1.6\,MgCha^{-1}yr^{-1}$ for Caxiuanã.

For comparison, Reich *et al.* (1998) found an average large tree dark respiration rate of $0.91 \pm 0.23\,\mu mol\,m^{-2}$ leaf area $s^{-1}$ for a slow-growing forest at San Carlos

del Rio Negro, Meir *et al.* (2001) reported a mean rate of $0.36 \pm 0.20 \,\mu\mathrm{mol\,m^{-2}}$ leaf area s$^{-1}$ for Jaru, SW Amazonia, and Cavaleri *et al.* (2008) reported a mean dark respiration rate of $0.59 \pm 0.44 \,\mu\mathrm{mol\,m^{-2}}$ leaf area s$^{-1}$ at La Selva, Costa Rica.

In summary, leaf respiration is probably the largest single term in internal C budget, although determination of its exact magnitude remains complex. The estimated sampling uncertainty for Caxiuanã ($\pm 1.4 \,\mathrm{MgC\,ha^{-1}\,yr^{-1}}$) does not account for potential systematic uncertainties in process and scaling, and for the synthesis table we apply a more conservative uncertainty estimate of $\pm 4.0 \,\mathrm{MgC\,ha^{-1}\,yr^{-1}}$ to all sites.

### Missing terms

A number of components of NPP are challenging to measure and likely to be missed (Clark *et al.*, 2001a). These include the productivity of small trees and lianas [$<10 \,\mathrm{cm\,dbh}$; but this is partially compensated by overestimating the productivity of new recruits; see Malhi *et al.* (2004)], palms (that grow via an apical meristem), tree ferns, ground flora and epiphytes. Similarly, the autotrophic respiration of some of these components may be missed. Hence, our estimates of total NPP, GPP and respiration are likely to be underestimates. The potential significance of this underestimation can be tested by validating against independent gas exchange measurements of soil respiration and canopy gas exchange, which is one of the aims of this paper.

### Ecosystem GPP and $R_e$ (Table 12)

Above-canopy eddy covariance studies attempt to measure the net C flux or net ecosystem exchange (NEE) in and out of the forest canopy, and hence enable the estimation of ecosystem gross primary production (GPP) and ecosystem respiration ($R_e$), by consideration of amplitude of the diurnal cycle of net C flux [as outlined by Reichstein *et al.* (2005)]. The method relies on assuming that night-time flux data (or an appropriately filtered subset of these data) are reliable, and extrapolating into the daytime (usually on the basis of temperature) to estimate daytime respiration. The major uncertainties in this approach are (i) the estimation of night-time ecosystem respiration fluxes, which are highly problematic in calm tropical conditions, particularly within tall canopies which decouple sub-canopy air from above-canopy turbulence; and (ii) the assumptions behind extrapolation into daytime, in particular which measurement of temperature to use and how to account for photoinhibition of leaf respiration. The standard approach to extrapolating from night-time measurements (e.g. Reichstein *et al.*, 2005) ignores photoinhibition of leaf dark respiration and hence likely overestimates daytime ecosystem respiration. Recently, Hutyra *et al.* (2008) have applied a variety of approaches to estimating ecosystem respiration at the Tapajós site, comparing eddy covariance-derived estimates of respiration with those derived from bottom-up measurements. Once ecosystem respiration has be estimated, GPP can be calculated as

$$GPP = R_e - NEE, \qquad (1)$$

where a negative NEE indicates a net C flux into the forest canopy.

Uncertainty estimates are rarely reported for eddy covariance-derived estimates of GPP, and when reported, they tend to indicate stochastic or interannual variability, rather than any systematic uncertainty that can be considerable. One feature to note is the sensitivity of GPP estimates to uncertainty in $R_e$. If $R_e$ is underestimated (e.g. because of missing night-time fluxes), then GPP is also underestimated, by a magnitude approximately half that of the total underestimation in $R_e$. If daytime $R_e$ is overestimated (e.g. by

**Table 12** Estimates of ecosystem respiration and gross productivity (in $\mathrm{MgC\,ha^{-1}\,yr^{-1}}$)

| Site | Subsite | Years | GPP or $R_e$ | Authors |
|---|---|---|---|---|
| Manaus | K34 | | $R_e$: $31.8 \pm 3.8$ | Chambers *et al.* (2004) |
| | C14 | 1995–996 | GPP: 30.4 | Malhi *et al.* (1998) |
| Tapajós | k67 | 2002–2005 | GPP: $31.4 \pm 0.4$ | Hutyra *et al.* (2007) |
| | | | $R_e$: $32.5 \pm 0.4$ | |
| Caxiuanã | Tower plot | 1999 | GPP: 36.3 | Carswell *et al.* (2002) |
| | | | $R_e$: 30.7 | |
| | Tower plot | 2000–2003 | GPP: 37.9–40.4 | Malhi *et al.* (unpublished data) |
| | | | $R_e$: 27.1–27.4 | |
| | Drought control | 2001–2003 | GPP: 31.2 | Fisher *et al.* (2007) |

All are derived from flux towers except Fisher *et al.* (2007), which is based on canopy photosynthetic parameters and plant and soil hydraulics, integrated within a canopy model.
GPP, gross primary productivity; $R_e$, ecosystem respiration.

**Table 13** Synthesis of carbon cycling estimates

| Site | Manaus | Tapajós | Caxiuanã |
|---|---|---|---|
| *Net primary productivities (NPP)* | | | |
| 1. $NPP_{finelitter}$ | **3.6 ± 0.7** | **6.5 ± 0.7** | **3.8 ± 0.1** |
| 2. $NPP_{branch}$ | 1.0 ± 1.0 | 1.0 ± 1.0 | 1.0 ± 1.0 |
| 3. $NPP_{trunk}$ | **2.58 ± 0.06** | **3.76 ± 0.07** | **2.16 ± 0.55** |
| 4. $NPP_{coarseroot}$ | 0.8 ± 0.2 | 1.0 ± 0.3 | 0.7 ± 0.2 |
| 5. $NPP_{fineroot}$ | 2.1 ± 0.7 | **2.0 ± 0.3** | **2.2 ± 0.6** |
| 6. $NPP_{VOC}$ | **0.13 ± 0.06** | 0.13 ± 0.06 | 0.13 ± 0.06 |
| 7. $NPP_{AG}$ | 7.3 ± 1.3 | 11.4 ± 1.2 | 7.2 ± 1.1 |
| 8. $NPP_{BG}$ | 2.8 ± 0.7 | 3.0 ± 0.4 | 2.8 ± 0.6 |
| 9. $NPP_{total}$ | 10.1 ± 1.4 | 14.4 ± 1.3 | 10.0 ± 1.2 |
| 10. $F_{DOC}$ | **0.19 ± 0.07** | 0.0004 ± 0.0004 | 0.19 ± 0.07 |
| 11. $Mort_{AG}$ | **2.4 ± 0.1** | **2.7 ± 0.2** | **1.9 ± 0.3** |
| *Respiration (R)* | | | |
| 11. $R_{leaf}$ | **10.0 ± 4.0** | **7.4 ± 4.0** | **8.9 ± 4.0** |
| 12. $R_{stem}$ | **4.2 ± 1.0** | **3.8 ± 1.0** | **5.1 ± 0.5** |
| 13. $R_{root}$ | 5.6 ± 2.0 | **3.7 ± 0.8** | **7.4 ± 0.5** |
| 14. $R_{cwd}$ | 2.5 ± 0.3 | **4.5 ± 1.1** | 2.2 ± 0.4 |
| 15. $R_{autotrophic}$ | 19.8 ± 4.6 | 14.9 ± 4.2 | 21.4 ± 4.1 |
| 16. $R_{heterotrophic}$ | 9.6 ± 1.2 | 14.9 ± 1.4 | 9.4 ± 0.8 |
| 17. $R_{total}$ | 29.3 ± 4.7 | 29.8 ± 4.4 | 30.1 ± 4.2 |
| *Partitioning* | | | |
| 18. Total AG fraction | 0.72 ± 0.18 | 0.77 ± 0.19 | 0.67 ± 0.16 |
| 19. Total BG fraction | 0.28 ± 0.08 | 0.23 ± 0.05 | 0.33 ± 0.05 |
| *Gas exchange fluxes* | | | |
| 20. $R_{soil}$ | **12.1 ± 1.7** | **12.0 ± 0.6** | **13.5 ± 0.9** |
| 21. $R_{eco}$ | **31.8 ± 3.8** | **32.5 ± 0.4** | **27.3 ± 0.2** |
| 22. GPP | **30.4** | **31.4 ± 0.4** | **38.2 ± 2.0** |
| *Bottom-up scaling* | | | |
| 23. $R_{soil\ expected}$ | 12.6 ± 2.3 | 14.1 ± 1.2 | 14.6 ± 1.0 |
| 24. $GPP_{expected}$ | 29.9 ± 4.8 | 29.3 ± 4.4 | 34.4 ± 4.2 |
| *Carbon-use efficiencies (CUE)* | | | |
| 25. $CUE_{ecosystem}$ | 0.34 ± 0.10 | 0.49 ± 0.16 | 0.32 ± 0.07 |
| 26. $CUE_{stem}$ | 0.46 ± 0.15 | 0.56 ± 0.14 | 0.30 ± 0.10 |
| 27. $CUE_{root}$ | 0.27 ± 0.10 | 0.35 ± 0.07 | 0.28 ± 0.06 |
| *Allocation fractions* | | | |
| 28. $NPP_{finelitter}/GPP_{expected}$ | 0.12 ± 0.03 | 0.22 ± 0.04 | 0.12 ± 0.02 |
| 29. $NPP_{BG}/GPP_{expected}$ | 0.10 ± 0.03 | 0.10 ± 0.02 | 0.09 ± 0.02 |
| 30. $NPP_{branch,trunk}/GPP_{expected}$ | 0.12 ± 0.04 | 0,16 ± 0.04 | 0.10 ± 0.04 |

All productivities and fluxes are in $MgC\,ha^{-1}\,yr^{-1}$; fractions and CUE values are dimensionless.

AG, aboveground; BG, belowground; VOC, volatile organic compound; DOC, dissolved organic carbon; GPP, gross primary productivity. Values in bold are directly measured, other values are inferred as described in the text.

ignoring photoinhibition), then GPP is overestimated by an amount equal to the amount of photoinhibition.

Reported estimates of GPP and ecosystem respiration are summarised in Table 12. The reported error bars

are likely to be underestimates. At Manaus and Tapajós, $R_e \approx GPP$, with a possible difference of order $\sim 1\,MgC\,ha^{-1}\,yr^{-1}$ that would be a net C source or sink. At Caxiuanã, the flux-derived $R_e$ is much less than the GPP, reflecting the likelihood of missing night-time fluxes that are not accounted for by friction velocity corrections. Malhi *et al.* (unpublished data) speculate that proximity to a large body of water is a factor, creating stationary mesoscale circulations that transfer $CO_2$ laterally under almost all wind conditions. For the Caxiuanã drought control plot, Fisher *et al.* (2007) utilised a canopy ecophysiology model to integrate measurements of canopy photosynthetic parameters, microclimate and soil and plant hydraulics, to estimate GPP at $31.2\,MgC\,ha^{-1}\,yr^{-1}$, substantially lower than the tower-based estimate and closer to the other two sites.

### *Synthesis (Table 13)*

The values distilled from the studies above are synthesised in Table 13. Values in bold are directly measured, values in normal type are estimated as described in the text.

Considering the components of NPP first (Table 13; Fig. 3a), the total NPP at Manaus and Caxiuanã is similar at $10.1 ± 1.4$ and $10.0 ± 1.2\,MgC\,ha^{-1}\,yr^{-1}$, respectively, and significantly higher at Tapajós ($14.4 ± 1.3\,MgC\,ha^{-1}\,yr^{-1}$). The largest components of NPP are canopy production (leaf/flower/fruit/twig), followed by stem production. There is little evidence of any significant variation in BG NPP between sites (but estimated fine root turnover at Manaus is simply an average of the other two sites). Hence, the high NPP at Tapajós is entirely explained by a disproportionate allocation to AG production.

The components of autotrophic respiration (Fig. 3b) are much more challenging to quantify, and the largest source of uncertainty in our calculations. Total estimates of autotrophic respiration are $19.8 ± 4.6\,MgC\,ha^{-1}\,yr^{-1}$ (Manaus), $14.9 ± 4.2\,MgC\,ha^{-1}\,yr^{-1}$ (Tapajós), and $21.4 ± 4.1\,MgC\,ha^{-1}\,yr^{-1}$ (Caxiuanã). Leaf respiration is the largest component and the most uncertain. There are considerable methodological differences between sites in measurements of leaf and root respiration (outlined above) that may explain some of the difference between sites.

Such comprehensive measurements of C cycling at these sites enable two independent checks of self-consistency. Firstly, we can compare against measurements of soil respiratory $CO_2$ efflux. The expected soil respiration can be calculated from rates of C inflow into the soil.

$$R_{soil,expected} = R_{root} + R_{soil,het.} \qquad (2)$$

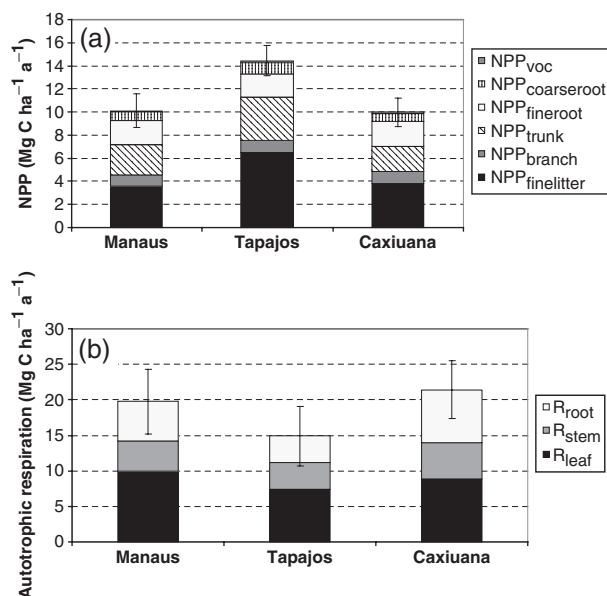If we assume quasiequilibrium conditions on an annual timescale and negligible interannual variability, the soil

**Fig. 3** Components of net primary productivity (a) and auto-trophic respiration for each site (b) in $MgC\,ha^{-1}\,yr^{-1}$. Error bars are standard errors of overall totals.

heterotrophic respiration is

$$R_{soil,het.} = NPP_{fineroot} + NPP_{finelitter} + F_{(cw-soil)}$$
$$\times (NPP_{trunk} + NPP_{branch}) + NPP_{BG} - \Delta C - F_{DOC}, \tag{3}$$

where $F_{(cw-soil)}$ is the fraction of CWD that is transferred to the soil (estimated as $0.24 \pm 0.15$ above) and $\Delta C$ is the change in soil C stocks. We assume there is negligible change in soil C stocks (i.e. $\Delta C \ll R_{soil}$), an assumption suggested for Tapajós by radiocarbon studies (Telles *et al.*, 2003), and the resulting calculations of expected $R_{soil}$ are listed in Table 13 and plotted in Fig. 4a. The largest contributors to soil respiration are fine litter, which is fairly well quantified, and root respiration, which carries greater methodological uncertainty. The material derived from CWD is a relatively minor component, and hence assumptions about the exact value of $F_{cw-soil}$ are not particularly important. When expected soil respiration is plotted against measured soil respiration (Fig. 3c), there is a fair consistency between approaches increasing confidence that our understanding of the BG C cycle is fairly complete. Agreement is particularly good at Manaus, but at the other two sites there some suggestion that less respiration is being measured than expected.

As a second crosscheck, we can calculate the GPP estimated from bottom-up measurements with those estimated from flux towers. The GPP of the forest is
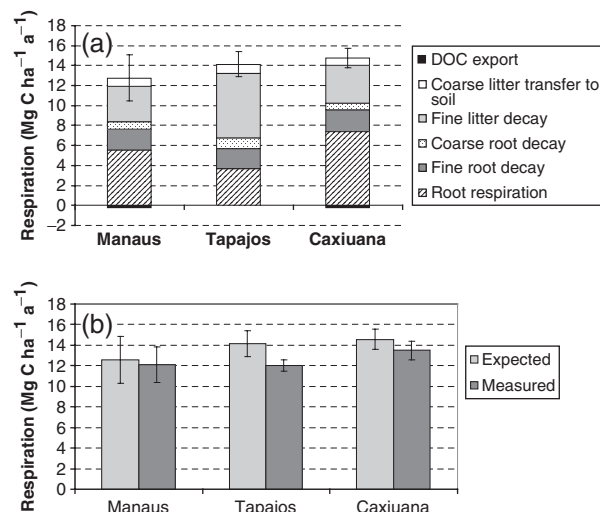


**Fig. 4** (a) Components of expected soil respiration, (b) compared with measured soil respiration fluxes, in $MgC\,ha^{-1}\,yr^{-1}$. Error bars are standard errors of overall totals.
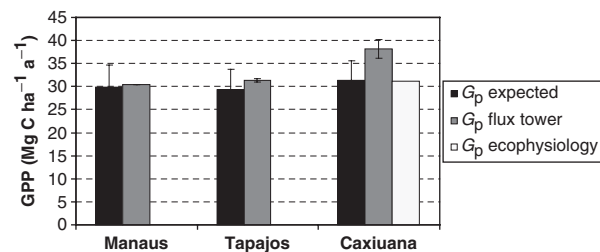


**Fig. 5** Calculated gross primary productivity (GPP) from component measurements compared with eddy covariance-derived estimates in $MgC\,ha^{-1}\,yr^{-1}$. For Caxiuanã, an independent estimate ($G_p$ ecophysiology) based on canopy photosynthetic parameters and plant and soil hydraulics is also shown (Fisher *et. al.*, 2007).

by definition the sum of net productivity and auto-trophic respiration:

$$GPP = NPP + R_{autotrophic}. \tag{4}$$

Hence, our predicted values of GPP (Table 13) are $29.9 \pm 4.8\,MgC\,ha^{-1}\,yr^{-1}$ (Manaus), $29.3 \pm 4.4\,MgC\,ha^{-1}\,yr^{-1}$ (Tapajós) and $31.4 \pm 4.2\,MgC\,ha^{-1}\,yr^{-1}$ (Caxiuanã). The error bars in these estimates are dominated by the large errors we ascribe to leaf respiration. When these estimates are compared with those from flux towers, the agreement is close, particularly for Manaus and Tapajós (Table 13; Fig. 5). At Caxiuanã, the flux tower estimate is substantially higher, but our estimate is almost identical to the Fisher *et al.* (2007) estimate ($31.2\,MgC\,ha^{-1}\,yr^{-1}$) derived from measured photosynthetic parameters and canopy hydrology. The dominant term in ecosystem respiration appears to be leaf respira-

tion, followed by root respiration, stem respiration and fine litter decomposition, all of roughly equal magnitude. It should be remembered that the tower-derived estimates assume no photoinhibition of leaf dark respiration; hence, the tower-based estimates of GPP may be underestimated by $\sim 3\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$, or the photoinhibition is offset by high daytime temperatures at the canopy top that are not accurately accounted for in the tower-derived estimations. Despite these caveats, the fairly close agreement between the two approaches (flux towers and bottom-up measurements) indicates there are no very large terms missing, such as enhanced respiration from branches, litter decomposition *in situ* in the canopy, understorey respiration, etc.

Note that this approach to GPP estimation and nomenclature differs from that applied by Litton *et al.* (2007) and some others. They choose to bypass the complexities of daytime leaf respiration, and only estimate night-time leaf respiration. The net daytime C exchange through leaves, which includes photosynthesis and photoinhibited dark respiration, is then considered as a single term, which they label GPP. While this approach has some merits, this nomenclature for GPP confounds two distinct physiological processes (photosynthesis occurring in chloroplasts and dark respiration occurring in mitochondria), and is perhaps better termed the *net daytime leaf C uptake*. The approach used here does at least attempt to consider only the photosynthetic cycle. Given these differences, it should be noted that the values of GPP reported by Litton *et al.*, should be expected to be smaller than those reported here (by an amount equal to photoinhibited daytime dark respiration, $\sim 2\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$) and those reported by most eddy covariance studies. There is still clearly a need to develop a coherent and agreed nomenclature around the determination of GPP.

It is now possible to calculate the ecosystem CUE, the fraction of GPP that is allocated to NPP.

$$\mathrm{CUE_{eco}} = \frac{\mathrm{NPP}}{\mathrm{GPP}} = \frac{\mathrm{NPP}}{\mathrm{NPP} + R_{\mathrm{auto}}} = 1 - \frac{R_{\mathrm{auto}}}{\mathrm{GPP}}. \quad (5)$$

It is also possible to calculate CUE separately for the stem and root components:

$$\begin{aligned} \mathrm{CUE_{stem}} &= \frac{\mathrm{NPP_{stem}}}{\mathrm{NPP_{stem}} + R_{\mathrm{stem}}}; \\ \mathrm{CUE_{root}} &= \frac{\mathrm{NPP_{BG}}}{\mathrm{NPP_{BG}} + R_{\mathrm{root}}} \end{aligned} \quad (6)$$

The values of $\mathrm{CUE_{eco}}$ at Caxiuanã ($0.32 \pm 0.07$) are similar to those at Manaus ($0.34 \pm 0.10$), confirming the picture of low CUE in old growth tropical forests suggested by Chambers *et al.* (2004) for Manaus. At Tapajós, however, $\mathrm{CUE_{eco}}$ is higher with a mean value of $0.49 \pm 0.16$, closer to the values reported in many temperate broadleaf forests (DeLucia *et al.*, 2007). Given the large error bars around the CUE estimates, however, the difference is not significant (*z*-test, $P = 0.14$). Fundamentally, this difference reflects the fact that the observations of higher wood and litter production at Tapajós are not matched by a higher GPP as seen by the flux tower.

Finally, we can calculate the proportion of GPP allocated to particular processes. Using our 'bottom-up' estimates of GPP, the fractions of GPP allocated to canopy production are $12 \pm 3\%$ (Manaus), $22 \pm 2\%$ (Tapajós) and $12 \pm 2\%$ (Caxiuanã), the fractions to root production are $10 \pm 3\%$ (Manaus), $10 \pm 2\%$ (Tapajós) and $9 \pm 2\%$ (Caxiuanã), and the fractions allocated to AG woody production (stems and branches) are $12 \pm 4\%$ (Manaus), $16 \pm 4\%$ (Tapajós) and $10 \pm 4\%$ (Caxiuanã).

## Discussion and conclusions

We have compiled available data and made some inductions to gain a fairly comprehensive understanding of internal C cycle of three forest stands in central and eastern Amazonia. The synthesis has shown that AG components are the largest contributors to NPP (70–80% of total NPP), and some terms (e.g. VOC production, DOC leakage) are relatively minor.

The crosschecking against soil chamber $CO_2$ efflux measurements and flux tower estimates shows good agreement between approaches, increasing confidence in all three approaches. The greatest measurement challenge is presented by autotrophic respiration, and by leaf respiration in particular. This has implications for the flux tower approach to estimating GPP: a 70% photoinhibition in leaf respiration is equivalent to a 23% reduction in ecosystem respiration, and thus GPP from flux towers may be underestimated. However, there is little evidence of significant increase or decrease in daytime ecosystem respiration rates (Hutyra *et al.*, 2007), and one possibility is that photoinhibition approximately offsets the temperature-related daytime increase of mitochrondial respiration from all ecosystem components.

There is a hint that there may be less soil respiration being measured than would be expected, particularly when considering that we are more likely to underestimate NPP components rather than overestimate them. Possible causes for this discrepancy may be methodological (e.g. the root disturbance during extraction at Caxiuanã may cause an overestimation of root respiration), but two other possibilities are (i) transport of dissolved $CO_2$ in sap flow (Levy *et al.*, 1999) or (ii) net uptake of soil C. Telles *et al.* (2003) present convincing evidence that there is little soil C increase in the top

soil layers, but some C accumulation in deeper, less C-saturated soil is still a possibility. A third possibility is that DOC export is greater than estimated, but the measurements of Waterloo *et al.* (2006) used here suggest that this is unlikely.

Recently, Cavaleri *et al.* (2006) reported enhanced $CO_2$ stem efflux in branches and small trees at a site in Costa Rica. If such a phenomenon were significant here, our estimates of stem and ecosystem respiration would be underestimated, yet our close agreements with flux towers suggests that we are not significantly under-estimating at the ecosystem level. One possibility is that enhanced crown $CO_2$ efflux reflects soil respired $CO_2$ that has been transported in the plant xylem. This would reduce soil $CO_2$ efflux while having no effect on ecosystem $CO_2$ efflux, as is observed.

*Variation among sites*

The observations at Caxiuanã (and updated values for Manaus) corroborate the observations of low CUE at Manaus noted by Chambers *et al.* (2004). Tapajós, however, has values closer to many temperate broadleaf systems, although the uncertainty around the estimate is large. The most plausible hypothesis to explain this difference is that there is likely to have been a significant mortality event in Tapajós in the 1990s (Pyle *et al.*, 2008), and that in the aftermath of the mortality there is a surge in growth with surviving individuals allocating disproportionately to wood production, causing an increase in CUE. The observation that GPP is no higher at Tapajós suggests that the enhanced AG production purely reflects a shift in C allocation to AG NPP, rather than an increase in total photosynthesis. The disturbance hypothesis is further supported by the selective logging experiment at km 83 in Tapajós (Figueira *et al.*, in press). In the aftermath of selecting logging, they report an increase in AG wood production that seems to be caused by increased light availability in small and medium trees, with little increase in overall ecosystem GPP. A similar result was reported by Chambers *et al.* (2004) following selective logging in the Bionte experiment. The fraction of GPP allocated to BG productivity seems very similar across all three sites.

A possible alternative hypothesis is related to the higher leaf and soil P and Ca content at Tapajós, although levels are still low by pan-tropical standards. The readily available P per unit mass of clay is relatively constant across the three plateau sites; hence, the higher nutrient status at Tapajós may be a product of the extremely high clay content of its soil (90%); clays present a much larger surface area on which to bind C and other nutrients. There is little difference in clay mineralogy between Tapajós and Manaus (both nacrite-dominated; C. A. Quesada, in press). Other possibilities include the possibility of nutrient input after the disturbance event, or an effect of the agricultural activity (and in particular liming) immediately upwind (east) of the km 67 tower, that may lead to enhanced deposition of Ca and P. Alternatively, this may be a trace of pre-Columbian agroforestry activity; there are numerous *terra preta* black earth sites located on bluffs above the Tapajós river, immediately to the west of the km 67 tower.

Mature lowland Amazonian forests are likely to be P-limited (Davidson *et al.*, 2007), with P availability possibly mediated by Ca and cation exchange capacity. More fertile sites in lowland Amazonia tend to favour fast growing, low wood density species (Baker *et al.*, 2004; Malhi *et al.*, 2004), which allocate more to wood and leaf production and less to structural and chemical defences and their associated metabolic costs.

Hence, either disturbance or high soil fertility appears to drive a shift towards increased CUE. Conversely, the low CUE observed at some tropical sites probably reflects either their old growth status or low soil fertility, and not their tropical climate, that is, high temperatures do not drive an increase in autotrophic respiration relative to photosynthesis. The phrase 'carbon use efficiency' is perhaps misleading at the level of an ecosystem: trees in a high CUE forest are no more 'efficient', they simply have different priorities in allocation of resources (more growth, less maintenance and defence) that reflect the environment they find themselves in. There is no advantage or goal in higher woody biomass production *per se*, only in the extent that it provides competitive advantage over neighbouring trees, decreases risk of mortality, etc. The fact that the observed CUE at Tapajós is similar to the values reported at many (younger) temperate broadleaf stands seems consistent with the recent review by DeLucia *et al.* (2007) that concluded that CUE tends to decline with stand age. The use of CUE $\sim 0.5$ in some ecosystem models seems a product of a bias towards recently disturbed temperature forests, (e.g. Waring *et al.*, 1998) and may be inappropriate for many tropical (and boreal) forests.

Considering the wider Amazon region, the greater wood production observed in more fertile, more dynamic western Amazonia may reflect an increase in GPP, or a shift in C allocation. Similarly, the decline in AG NPP with elevation observed in tropical montane forest may reflect decreased AG allocation or decreased photosynthesis. We are currently conducting similar comprehensive C cycling studies at a number of sites, including a fertile *terra preta* (Amazonian black earth) site in eastern Amazonia, dry forests in southern Amazonia, fertile lowland Amazonian forests in western Amazonia and along an elevation transect in the

Andes. The work presented here, and its validation against flux towers, gives increased confidence that such 'bottom-up' approaches to quantifying GPP and its allocation in the tropics are indeed valid and fairly complete, and can also be applied at sites where flux towers do not exist or would be inappropriate (e.g. a one hectare *terra preta* site, or in the steep topography of the Andes). Moreover, such measurements give a far more detailed and mechanistic understanding of the component processes. Results from these other sites will be reported in forthcoming papers.

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## Supporting Information

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

**Table S1.** Soil carbon content data for (a) Caxiuana, (b) Tapajos, (c) Manaus (Quesada *et al.*, in press)

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