

The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests

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Abstract

Understanding the relationship between photosynthesis, net primary productivity and growth in forest ecosystems is key to understanding how these ecosystems will respond to global anthropogenic change, yet the linkages among these components are rarely explored in detail. We provide the first comprehensive description of the productivity, respiration and carbon allocation of contrasting lowland Amazonian forests spanning gradients in seasonal water deficit and soil fertility. Using the largest data set assembled to date, ten sites in three countries all studied with a standardized methodology, we find that (i) gross primary productivity (GPP) has a simple relationship with seasonal water deficit, but that (ii) site-to-site variations in GPP have little power in explaining site-to-site spatial variations in net primary productivity (NPP) or growth because of concomitant changes in carbon use efficiency (CUE), and conversely, the woody growth rate of a tropical forest is a very poor proxy for its productivity. Moreover, (iii) spatial patterns of biomass are much more driven by patterns of residence times (i.e. tree mortality rates) than by spatial variation in productivity or tree growth. Current theory and models of tropical forest carbon cycling under projected scenarios of global atmospheric change can benefit from advancing beyond a focus on GPP. By improving our understanding of poorly understood processes such as CUE, NPP allocation and biomass turnover times, we can provide more complete and mechanistic approaches to linking climate and tropical forest carbon cycling.

Keywords: allocation, carbon cycle, carbon use efficiency, drought, gross primary productivity, net primary productivity, residence time, respiration, root productivity, tropical forests

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Introduction

What processes and drivers determine the spatial variation in growth rate and biomass of forest ecosystems

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and how are these processes responding to global atmospheric change? In trying to understand and predict the growth and biomass of forest ecosystems, much research and discussion has focused on two key features, namely understanding controls on photosynthesis and the accompanying process of carbon

assimilation into ecosystems (Landsberg & Sands, 2010) and alternatively, quantifying the structure and spatial variation of woody biomass (Pan *et al.*, 2013). As examples of the focus on photosynthesis, (i) optical remote sensing methods relate various metrics of greenness or photosynthetic activity to infer rates of photosynthesis (Running *et al.*, 2004), (ii) the global network of carbon dioxide (CO₂) flux towers conducts observations of the exchange of CO₂ between canopies and the atmosphere to infer controls on photosynthesis, respiration and net carbon balance (Law *et al.*, 2002; Zhao *et al.*, 2005; Beer *et al.*, 2010), and (iii) global land-surface models have a particular focus on representing how temperature, drought and CO₂ serve as controls of photosynthesis in the context of global change (Galbraith *et al.*, 2010; Marthews *et al.*, 2012; Huntingford *et al.*, 2013). As examples of the focus on quantifying woody biomass, forest inventories convert tree diameter, wood density and height estimates into estimates of spatial variation in biomass (Mitchard *et al.*, 2014) and so may also quantify long-term changes in forest carbon balance (Lewis *et al.*, 2009; Phillips *et al.*, 2009), while radar and LiDAR-based remote sensing approaches estimate and map biomass and infer controls on forest processes (Saatchi *et al.*, 2007; Asner *et al.*, 2012). There is much merit in the research on photosynthesis and biomass, and much still to be learned. However, there are also a considerable number of intermediate processes that link photosynthesis and biomass, which receive relatively little scientific attention and yet are equally or even more important for understanding controls on the growth and biomass of tropical forest ecosystems (Fig. 1).

For instance, it is frequently assumed that there is a fairly direct link between photosynthesis and woody

growth rates and biomass (e.g. increasing water deficit leads to reduced photosynthesis, which leads to slower growth and lower biomass; Nepstad *et al.*, 2002). As another example, rising CO₂ may stimulate photosynthesis, which in turn is expected to stimulate woody growth rates and lead to an increase in forest biomass and a net biomass carbon sink (Lewis *et al.*, 2004). Conversely, changes in growth rates are often interpreted as directly signifying changes in net primary productivity (e.g. Feeley *et al.*, 2007) and such an assumed relationship forms a basis for inferences in dendrochronology. Figure 1 explores this chain of causality in more detail (Malhi, 2012):

1. The energy locked into carbon bonds through annual photosynthesis (gross primary productivity or GPP) is partially (50–70%) used for plant metabolic processes (i.e. autotrophic respiration used for growth or maintenance, with accompanying release of CO₂), and partially (30–50%) used for the net production of biomass (i.e. net primary productivity or NPP) (Marthews *et al.*, 2012).
2. The net primary productivity is allocated between various organs, in particular woody tissue, fine roots, canopy leaves, flower and fruit. In tropical forest ecosystems, typically only around 30–50% of NPP is allocated to woody growth (Malhi *et al.*, 2011).
3. The relationship between woody growth and biomass is not direct. The standing live woody biomass of an ecosystem is a result of both input (woody biomass recruitment and growth) and output (mortality). A key feature of tropical forests, in contrast to the human-disturbed temperate forests and fire-disturbed boreal forests, is that many of them are relatively old-growth stands. The processes of tree recruitment/growth and mortality are of approximately equivalent magnitude in such forests, and this can be expressed in terms of a woody biomass residence time (τ_w), which can be calculated as equal to above-ground woody biomass divided by above-ground woody productivity (Galbraith *et al.*, 2013).

The relative importance of these intermediate factors in influencing the relationship between photosynthesis and biomass is rarely examined. To explore them, it is necessary to quantify the major components of autotrophic respiration, of NPP and its allocation, and woody biomass residence time. In other words, it is necessary to generate a comprehensive description of the autotrophic carbon cycle.

Here, we focus our analysis on the lowland tropical forests of Amazonia (Fig. 2), probably the best studied of the major tropical forest regions. Previously, Malhi *et al.* (2009) synthesized data for three eastern Amazonian forests with similar climate and soil regimes to

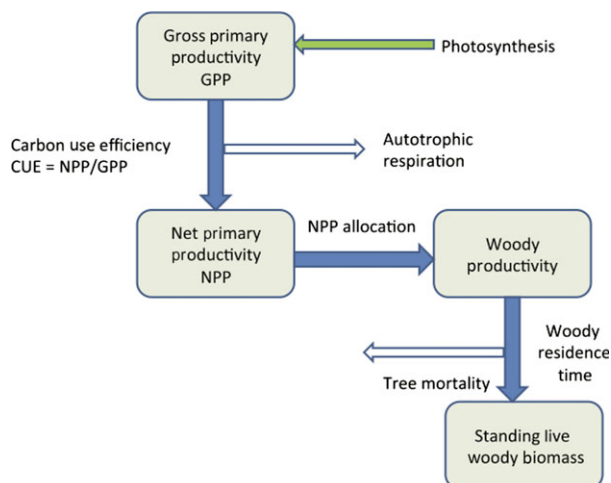


Fig. 1 The source-to-sink pathway leading from photosynthesis to standing live woody biomass (Malhi, 2012).

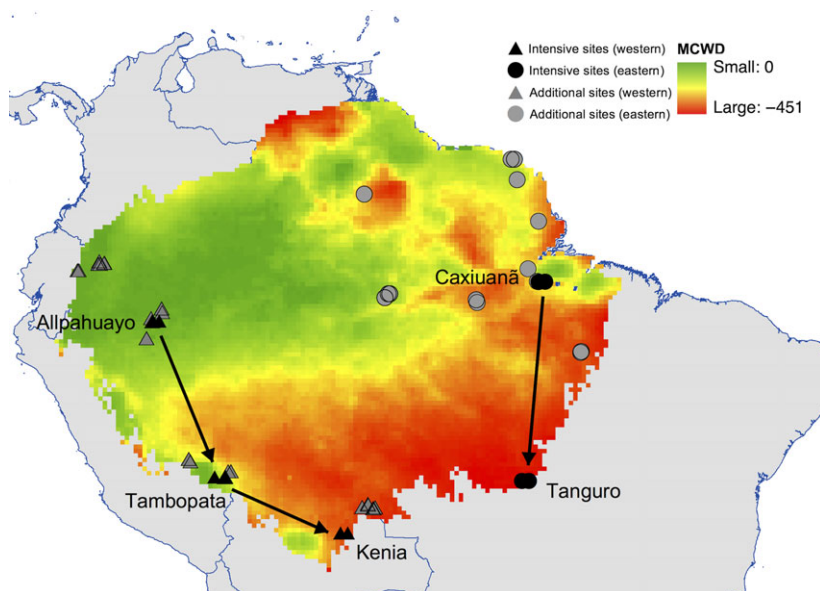


Fig. 2 The location of study sites in eastern and western Amazonia, with arrows indicating the two wet–dry gradients. Sites are superimposed on a gridded map of mean maximum climatological water deficit (MCWD, mm). Black symbols indicate intensive carbon cycle sites in western (triangles) and eastern (circles) Amazonia. Grey symbols indicate a wider dataset of forest plots used for residence time calculations.

describe their full carbon cycle, including estimates of GPP and CUE. Working on a wider Amazonian scale, Aragão *et al.* (2009) published data on NPP and its allocation for ten plots ranging through Brazil, Colombia and Peru. Thus far, no study has combined these two aspects to examine the full autotrophic carbon budget (as in Malhi *et al.*, 2009) at a scale that begins to capture the variation of soil and climate conditions across Amazonia.

Here, we study how autotrophic carbon cycle processes vary across lowland Amazonian forests to examine fundamental questions and assumptions about the linkages between photosynthesis, productivity and growth in old-growth tropical forest ecosystems. In particular, we contrast the carbon budgets of humid and seasonally dry tropical forests to better understand the influences of rainfall regime on GPP, NPP, woody growth and biomass. To do so, we use a global network of sites where the components of the carbon cycle are being monitored in detail, the Global Ecosystems Monitoring (GEM) network (gem.tropicalforests.ox.ac.uk), a subset of the Amazon forest inventory network RAINFOR (www.rainfor.org, Malhi *et al.*, 2002; Phillips *et al.*, 2009). We have recently completed detailed descriptions of the carbon cycle at 16 RAINFOR-GEM plots in Amazonia (del Aguila-Pasquel *et al.*, 2014; Araujo-Murakami *et al.*, 2014; da Costa *et al.*, 2014; Doughty *et al.*, 2014; Malhi *et al.*, 2014; Rocha *et al.*, 2014). This represents the single most comprehensive

effort in tropical forests to date, but there has been no multisite analysis of these data. Here, we synthesize results from the subset of these plots that cover lowland old-growth forests (10 plots across five sites, incorporating 480 plot-months of intensive data collection). The data set was stratified into two gradients, one set of plots in western Amazonia with relatively fertile but poorly structured soil, and one set of plots in eastern Amazonia with infertile but better structured soils (Quesada *et al.*, 2010, 2012), where each set of plots varies in its seasonal water deficit. Our intent is not to scale from these plots to the whole of the Amazon, but rather to illustrate the importance of a full plant carbon budget perspective by asking the following questions:

1. To what extent can key stand-level aspects of the lowland Amazon forest carbon cycle (such as GPP, NPP, CUE, and NPP allocation to canopy, wood, stem growth and fine roots) be predicted from rainfall patterns and from soil properties?
2. Can net primary productivity or woody growth be reliably predicted from GPP, and, conversely, is the woody growth of a tropical forest stand a useful proxy for its NPP or GPP? If not, why not?
3. What is the relative importance of different aspects of the carbon budget (GPP, CUE, NPP allocation and residence time) in determining spatial variation in biomass in Amazonian tropical forests?

Table 1 Environmental characteristics of 1 ha study sites occurring along wet–dry gradients in eastern and western Amazonia. Data for radiation, temperature, precipitation and MCWD are available for each pair of sites

	Western Amazonia Transect					Eastern Amazonia				
	Allpahuayo A	Allpahuayo C*	Tambopata V	Tambopata VI	Kenia Wet	Kenia Dry	Caxiuana Control	Caxiuana Tower	Tanguro Control†	Tanguro Burn†
RAINFOR site code	ALP11/ALP12	ALP30	TAM05	TAM06	KEN01	KEN02	CAX04	CAX06	–	–
Latitude	–3.95	–3.9543	–12.8309	–12.8385	–16.0158	–16.0158	–1.7160	–1.7369	–13.0765	–13.0765
Longitude	–73.4333	–73.4267	–69.2705	–69.2960	–62.7301	–62.7301	–51.4570	–51.46194	52.3858	52.3858
Elevation (m asl)	120	150	223	215	384	384	47	47	385	385
Solar radiation (GJ m ^{–2} yr ^{–1})	5.2	5.2	4.8	4.8	5.9	5.9	5.7	5.7	6.74	6.74
Mean annual air temperature (°C)	25.2	25.2	24.4	24.4	23.4	23.4	25.8	25.8	25.0	25.0
Precipitation (mm yr ^{–1})	2689	2689	1900	1900	1310	1310	2311	2311	1770	1770
Mean MCWD (mm)	–6	–6	–259	–259	–386	–386	–203	–203	–482	–482
Soil moisture (%)	26.8 ± 0.3	10.8 ± 0.2	21.8 ± 0.2	35.5 ± 0.4	19.7 ± 0.4	16.0 ± 0.3	22.4 ± 0.1	27.1 ± 0.3	10.7 ± 0.2	10.8 ± 0.2
Soil type	Alisol/Gleysol	Arenosol	Cambisol	Alisol	Cambisol	Cambisol	Vetic Acrisol	Ferralsol	Ferralsol	Ferralsol
P _{total} (mg kg ^{–1})	125.6	37.6	256.3	528.8	447.1	244.7	37.4	178.5	147	147
Total N (%)	0.1	0.08	0.16	0.17	0.22	0.17	0.06	0.13	0.16	0.16
Total C (%)	1.19	1.13	1.51	1.20	2.4	2.00	0.83	1.68	2.55	2.55
Soil C stock (Mg C ha ^{–1} from 0 to 30 cm)	92.95	16.4	43.7	37.4	74.8	67.1	35	51.9	67.1	67.1
Soil organic layer depth (cm)	12	10	13	37	32	54	30	35	28	28
Cation exchange capacity (mmol _c kg ^{–1})	30.4	4.9	44.8	56.8	75.58	60.74	1.34	22.82	19.47	19.47
Sand (%)	65	82	40	2	58.05	55.48	83.69	32.54	45.73	45.73
Clay (%)	15	2	44	46	19.13	18.25	10.68	53.76	48.9	48.9
Silt (%)	20	16	17	52	22.82	26.27	5.64	13.7	5.37	5.37

*This site is located on an infertile, sandy upper soil layer; however, there is evidence that tree roots may have access to a deeper, more fertile soil and thus contribute to the high productivity observed (P.V.A. Fine, personal communications).

†Soil data derived from a neighbouring site.

4. Are the relatively low values of biomass in seasonally dry tropical forests caused by a decrease in GPP and woody growth rates, or an increase in mortality rates?

Materials and methods

Field sites

We collected several years of data on productivity, autotrophic respiration and components of the carbon budget from 10 plots at five sites (two plots per site) in contrasting rainfall and soil regimes in Amazonia (Table 1; Fig. 2). Underlying data will be made available at the GEM network website (<http://gem.tropicalforests.ox.ac.uk/data>). The western Amazonian sites ranged from NE Peru (no dry season; del Aguila-Pasquel *et al.*, 2014), through SE Peru (moderate dry season; Malhi *et al.*, 2014) to Bolivia (strong dry season; Araujo-Murakami *et al.*, 2014), which is located on the ecotone between humid Amazon forest and *chiquitano* dry forest. The eastern Amazonian sites ranged from humid forest in NE Amazonia (da Costa *et al.*, 2014) to dry forest in SE Amazonia (Rocha *et al.*, 2014), which sits close to the dry forest-savanna ecotone. The western Amazonian sites are on relatively fertile soils, while the eastern sites are on very infertile soils (Table 1). Western Amazonian soils generally have weaker physical structure, which may also affect forest mortality rates and turnover times (Quesada *et al.*, 2012). The plots included in this analysis (except one fire experiment plot; Appendix S1) show little evidence of anthropogenic disturbance of the forest community structure, hosting mixed-age tree communities with little net increment in biomass.

The small distance (typically a few km) between the two plots at each site could lead to issues of pseudoreplication. However, there are sufficient differences in both soil conditions and species composition within each pair to consider them independent sample points. At the NE Peru site (Allpahuayo), one plot is on white sand, while the other is on predominantly clay soils (del Aguila-Pasquel *et al.*, 2014), resulting in very different species composition. Likewise, at the SE Peru site (Tambopata), one plot is in a palm-rich forest on Holocene floodplain, while the other is on an older Pleistocene terrace (Malhi *et al.*, 2014). At the Bolivia site (Kenia), the plot on deeper soils has a species composition typical of humid Amazonian forest, whereas the plot on shallow soils is typical of dry *chiquitano* forests (Araujo-Murakami *et al.*, 2014). At the NE Brazil site (Caxiuanã), one plot is on clay soils and the other on a sandy loam, with accompanying contrasts in species composition. At the SE Brazilian Amazonia site (Tanguro), there is greater similarity in species composition, but one plot experiences fire every year and the other site every few decades (Rocha *et al.*, 2014).

For the analysis of residence time and woody biomass, and to place our intensive plots in a regional context, we include the lowland Amazonian component of a larger biomass and woody growth rate data set (Fig. 2; $n = 82$ plots) reported by Galbraith *et al.* (2013). All sites studied are mixed-age forests

with little evidence of nonequilibrium size structure. It is possible that fire dynamics at a multidecadal scale has had some influence on the driest sites (Kenia and Tanguro: Araujo-Murakami *et al.*, 2014; Rocha *et al.*, 2014).

Field methods

We adopt the field protocol of the GEM network (<http://gem.tropicalforests.ox.ac.uk>). Methods are described in detail in a manual on the website, as well as in the site-specific papers cited above and are summarized here only briefly.

The protocol measures and sums all major components of NPP and autotrophic respiration on monthly or seasonal time-scales in each 1 ha forest plot (for site-specific details see Table S1 and Appendix S1). For NPP, this includes canopy litterfall (NPP_{canopy}) from litterfall traps at bimonthly to monthly intervals, estimates of leaf loss to herbivory from scans of litterfall, above-ground coarse woody productivity (NPP_{ACW}) of all medium-large (≥ 10 cm dbh) trees in the plot and small trees (2–10 cm dbh) in subplots via dendrometers at regular intervals, the turnover of branches on live trees by conducting transect censuses every 3 months of freshly fallen branch material from live trees, fine root productivity ($NPP_{\text{fine root}}$) from ingrowth cores installed and harvested every 3 months, and estimation of coarse root productivity by applying a multiplying factor to above-ground woody productivity. For autotrophic respiration, rhizosphere respiration is estimated by subtracting the respiration of root-free soil from that of unaltered soil, above-ground woody respiration is estimated by measuring stem respiration on monthly timescales and scaling to the stand level by estimating stem surface area, below-ground coarse root and bole respiration is estimated by applying a multiplier to R_{stem} and leaf dark respiration by measuring leaf dark respiration rates on sunlit and shaded leaves in two seasons, then scaling by estimates of sun and shade leaf fractions and applying a correction of light inhibition of dark respiration. We recognize that many of these measurements have potential systematic uncertainties: we assign sampling or systematic uncertainties to each measurement, and rigorously propagate by quadrature the uncertainties through our calculations (Appendix S1).

The measured components of NPP and R_a are then summed to estimate total NPP and autotrophic respiration R_a (Appendix S1). In plant-level autotrophic steady state conditions (and on annual timescales or longer where there is little net non-structural carbohydrate storage), gross primary productivity (GPP), the carbon taken up via photosynthesis, should be approximately equal to plant carbon expenditure (PCE), the amount of carbon used for NPP and autotrophic plant respiration (R_a) if there is no net accumulation or loss of nonstructural carbohydrates. Autotrophic steady-state condition does not require the total plot carbon cycle to be in equilibrium, the plot can still be gaining or losing biomass or soil carbon stocks, as long as there is no substantial accumulation or loss of non-structural carbohydrates. Hence, we estimated GPP as the sum of NPP and R_a . We calculate the carbon use efficiency (CUE) as the proportion of total GPP invested in NPP rather than R_a :

$$\text{CUE} = \frac{\text{NPP}}{\text{GPP}} = \frac{\text{NPP}}{\text{NPP} + R_a} \quad (1)$$

Our biometric estimate of GPP is indirect and depends on summing up components of NPP and R_a , each with their inherent sampling errors and systematic uncertainties. An alternative approach to estimating GPP (also with inherent errors) is from eddy covariance flux measurements. Comparisons of biometric approaches with flux- or canopy ecophysiology in six sites (five tropical and one temperate broadleaf) demonstrate good agreement (Table S2, Fig. S1; slope = 0.97 ± 0.04 , coefficient of determination = 0.61), suggesting that no major terms of the autotrophic carbon budget are being missed.

Somewhat inevitably, any estimate of NPP may be biased towards underestimation because it neglects several small NPP terms, such as NPP lost as volatile organic emissions, nonmeasured litter trapped in the canopy or dropped from understorey plants below the litter traps. At a site in central Amazonia, volatile emissions were found to be a minor component of the carbon budget ($0.13 \pm 0.06 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; Malhi *et al.*, 2009). For below-ground NPP, the allocation to root exudates and to mycorrhizae is neglected. In effect, we treat root exudation and transfer to mycorrhizae as rhizosphere autotrophic respiration rather than as NPP, which could potentially impact our CUE estimates. Given that these exudates are labile and rapidly respired by mycorrhizae and soil microfauna in the rhizosphere, this exudate NPP term is very similar to fine root autotrophic respiration in terms of carbon cycling. The fairly close agreement with independent estimates of GPP (Fig. S1; Table S2) suggests that there are no large missing terms or biases at the scale of the whole stand.

Because our estimate of NPP includes only straightforward biomass production terms and neglects mycorrhizae, exudates and VOCs, it has recently been proposed that CUE should be termed the biomass production efficiency (BPE; Vicca *et al.*, 2012). Here, we retain the use of CUE to be compatible with the wider and older literature, but note that our CUE is equivalent to BPE. At the few tropical sites where the mycorrhizal component of rhizosphere respiration has been evaluated, it has values around $1\text{--}2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (L.K. Kho, Y. Malhi, S. Tan, unpublished results; D.B. Metcalfe, unpublished results). This suggests that site-to-site variations in mycorrhizal activity are likely to contribute to a mismatch $<1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ between biomass production and total NPP.

It is important to note that our calculation of NPP is based on the summation of four independent measurements (litterfall, tree growth, fine root production and branchfall), and our estimate of GPP is based on the summation of seven independent measurements (the components of NPP, as well as leaf, stem and rhizosphere respiration measurements). While some of these terms can carry substantial measurement and scaling uncertainties, if the uncertainties are independent for each measurement, some of these uncertainties potentially cancel one another and they propagate by quadrature to result in a manageable uncertainty in the final sum NPP or GPP (Appendix S1). For example, while there may be significant uncertainty in our measurement of root productivity or in our

scaling of stem respiration, this does not result in unmanageable uncertainties in our estimates of GPP. By contrast, an eddy covariance-based estimate of GPP is based on a single type of measurement (of net ecosystem exchange); hence, any uncertainties in the method, such as underestimation of nighttime respiration in stable atmospheric conditions, can result in an equivalent uncertainty in the final estimate of GPP. Hence, it could be argued that a carbon summation measurement comprised of seven independent measurements may potentially be more accurate than an eddy covariance-based estimate comprised of one measurement. Where the two approaches agree (as for many of the sites in Fig. S1), we can have increased confidence that both approaches are capturing the major components of the carbon cycle.

In addition to measuring major components of the autotrophic carbon cycle, we measured precipitation at each location, using local automatic weather stations gap-filled with other weather station data and satellite rainfall products where necessary. Mean maximum climatological water deficit (MCWD), a measure of peak dry season water deficit, was then calculated following Aragão *et al.* (2007). We prefer the use of MCWD, rather than more traditional annual precipitation, because it is a simple metric of dry season intensity and therefore more closely linked to the mechanisms (e.g. water deficits that lead to stomatal closure, leaf shedding, etc.) that limit GPP.

The data set presented represents the largest methodologically controlled analysis of carbon cycling for lowland tropical forests to date. Despite this, the number of plots analysed is low ($n = 10$) and as discussed above, may be at risk of spatial autocorrelation; caution is warranted in interpretation. Thus, we apply statistical analysis to the data set as a whole, but do not report statistics for individual regions ($n = 6$ in west and $n = 4$ in east) unless significance is very high.

Analysis framework

To examine what parameters explain the variation in total NPP, above-ground coarse wood productivity (NPP_{ACW} ; a proxy for tree growth rates) and above-ground biomass among sites, we present a systematic framework to decompose the relationship between NPP_{ACW} and GPP into several terms in a productivity–allocation–turnover chain. As defined here, NPP_{ACW} includes the net recruitment and growth of small and large trees as calculated from allometric equations, but excludes branch turnover – hence it is equivalent to the above-ground coarse woody productivity most usually determined from multiple censuses of forest plots (e.g. Malhi *et al.*, 2004). The framework follows as

$$\text{NPP} \equiv \text{GPP} \times \frac{\text{NPP}}{\text{GPP}} \quad (2)$$

$$\text{i.e. } \text{NPP} \equiv \text{GPP} \times \text{CUE}$$

$$\text{NPP}_{\text{ACW}} = \text{GPP} \times \frac{\text{NPP}}{\text{GPP}} \times \frac{\text{NPP}_{\text{ACW}}}{\text{NPP}} \quad (3)$$

$$\text{i.e. } \text{NPP}_{\text{ACW}} = \text{NPP} \times \text{fractional allocation to above-ground wood}$$

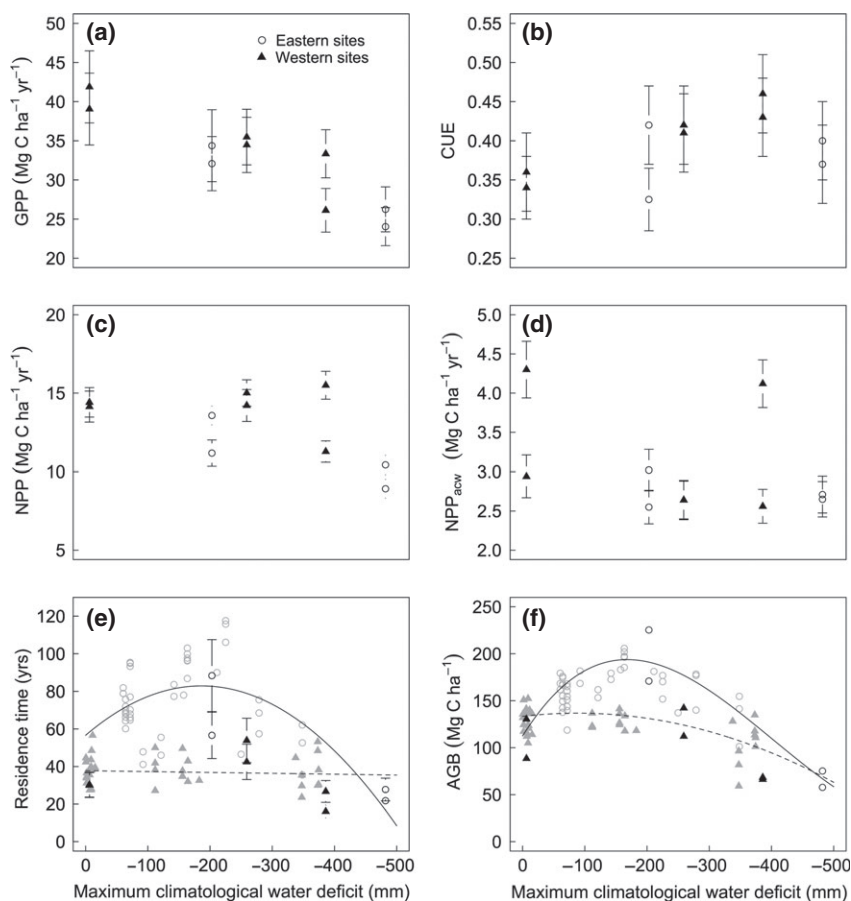


Fig. 3 Productivity, allocation and carbon stock variables plotted as a function of mean maximum climatological water deficit (MCWD): (a) gross primary productivity (GPP); (b) carbon use efficiency (CUE); (c) net primary productivity (NPP); (d) fractional NPP allocation to above-ground coarse wood, excluding branch turnover; (e) coarse woody biomass residence time, with the two low MCWD sites overlapping in means and error; (f) above-ground woody biomass. Black symbols indicate intensive measurement sites, grey symbols a wider forest inventory data set. Curves illustrate global fits for eastern (solid) and western (dashed) data sets. Bars indicate ± 1 SE.

For a mature forest, where biomass growth and mortality rates are similar and there is little net change in biomass, the above-ground woody biomass residence time (τ_w) can be estimated as woody biomass divided by woody productivity (Galbraith *et al.*, 2013). Hence, biomass can be expressed as:

$$\text{Biomass}_{\text{ACW}} \equiv \text{GPP} \times \frac{\text{NPP}}{\text{GPP}} \times \frac{\text{NPP}_{\text{ACW}}}{\text{NPP}} \times \tau_w \quad (4)$$

The biomass residence time is largely determined by the mortality rates of medium and large trees. However, because large tree mortality events are stochastic and may be poorly captured by 1 ha plots, we use standing biomass and woody growth rates to determine residence times. The assumption is that over appropriate timescales (~ 10 years), the woody production and mortality are approximately equal (i.e. the forest is not significantly increasing in biomass compared to its standing biomass). However, woody production rates show much less variability than mortality at interannual scales, and hence better represent the mean mortality rate (in biomass terms) of a 1 ha plot. If the plot is still substantially aggrading

(e.g. after a disturbance), our assumption will tend to underestimate residence time.

We analysed the relationship between various components of the carbon cycle as a function of maximum climatological water deficits (MCWD), east vs. west region and the interaction of the two by means of general linear models. For CUE and carbon allocation fractions, a logit link function was specified. For those response variables with a normal error structure (GPP, NPP, AGB, τ_w), an identity link function was specified. The minimal adequate model was chosen by stepwise evaluation using AIC. All analyses were conducted in R 3.0.1 (R Core Team, 2013).

Results

Among the western (fertile) sites, mean annual precipitation (MAP) ranged from 1310 to 2689 mm yr^{-1} , while seasonal differences in the timing of the precipitation resulted in a maximum climatological water

deficit (MCWD) ranging from -6.2 mm (no dry season) to -386 mm (strong dry season; Table 1). The eastern (infertile) sites varied similarly, with MAP ranging from 1770 to 2311 mm and MCWD from -203 mm (moderate dry season) to -482 mm (very strong dry season).

Estimates of carbon cycle components are presented in Table S3. GPP demonstrates a clear and significant negative relationship with increasing water deficit, declining from around 40 Mg C ha⁻¹ yr⁻¹ in the sites with the lowest MCWD to around 25 Mg C ha⁻¹ yr⁻¹ at the sites with the highest MCWD ($P < 0.001$, Fig. 3a). There is no significant effect of soil regime (as delineated by the east vs. west sites) on GPP ($P > 0.1$).

There is no significant overall relationship between CUE and MCWD ($P > 0.1$, Fig. 3b). We also detected no significant effect of soil regime (east vs. west) on CUE ($P > 0.1$). However, in the western (fertile) sites,

CUE shows a steady and significant increase with increasing (more negative) MCWD, ranging from around 0.35 in the least seasonal sites, to around 0.41 in the moderately seasonal sites, to around 0.45 in the driest sites (least squares regression: $r^2 = 0.91$; $P = 0.002$; Fig. 3b). Hence, the decline in GPP with increasing seasonality is largely offset by the increase in CUE (i.e. a greater reduction in R_a), leading to no significant relationship between NPP and MCWD or soil regime (Fig. 3c). To compare with literature where annual precipitation is used rather than MCWD, we reproduce an equivalent to Fig. 3, but plotted against annual precipitation, in supplementary material (Fig S2). As expected, the relationship between GPP and MCWD is stronger than that with annual precipitation (Fig S2a).

Figure 4a plots the relationship between NPP and GPP. In recognition of the autocorrelation between these two variables, our main purpose here is not to establish

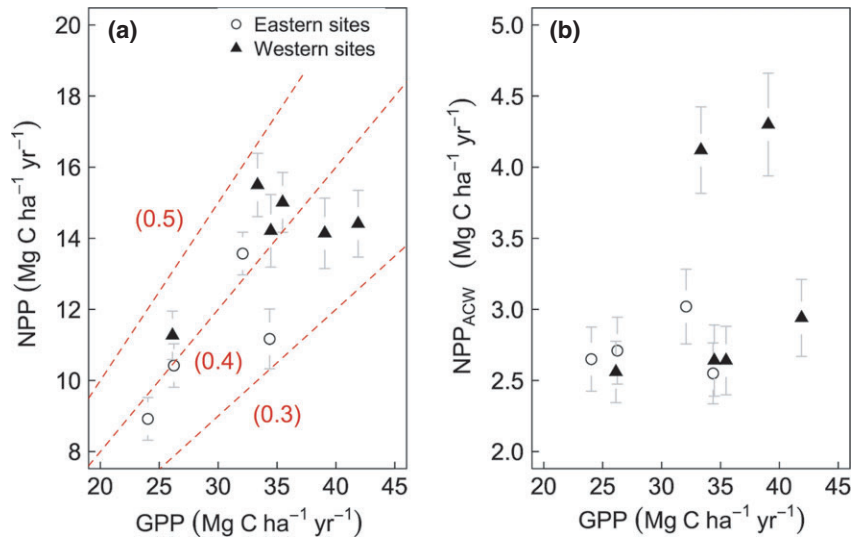


Fig. 4 Relationship between (a) total NPP and (b) above-ground coarse woody NPP as a function of GPP. Dotted lines in (a) reflect carbon use efficiencies (CUE) of 0.3, 0.4, and 0.5. Bars indicate ± 1 SE.

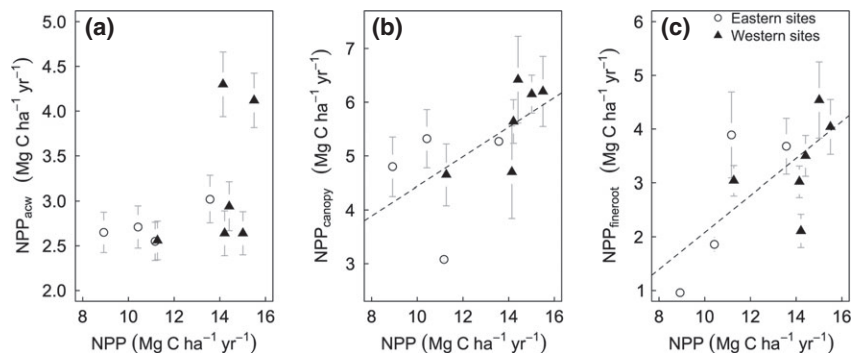


Fig. 5 Various components of net primary productivity as a function of total net primary productivity: (a) above ground NPP; (b) canopy NPP; (c) fine root NPP.

the significance of relationships, but to illustrate the range of values possible among the ten different plots. When the linear regression is forced through the origin, the mean slope (CUE) of the data set is 0.39 ± 0.01 . However, there is substantial residual variance in CUE among sites. This is particularly noticeable in the fertile western sites, where the GPP ranges between 34 and 42 Mg C ha⁻¹ yr⁻¹ in five of the six plots (CUE between 0.34 and 0.46), with no corresponding trend in NPP.

Within this data set, there is no evidence for significant relationships between the components of NPP allocation (to wood, canopy or fine roots) and MCWD (Fig. S3). Hence, above-ground wood production NPP_{ACW} (Fig. 3d) is similar at all sites. This term is equivalent to the above-ground woody production term most frequently estimated from forest inventories (Malhi *et al.*, 2004). NPP_{ACW} shows no significant relationship with NPP or GPP (Figs 4b and 5; $P > 0.05$), while total canopy production ($r^2 = 0.31$, $P < 0.06$) and fine root production ($r^2 = 0.41$, $P < 0.03$) have more significant relationships to overall NPP (Fig. 5). Hence, woody growth is a particularly poor proxy for total NPP. Again, there is potential for autocorrelation here as NPP_{ACW} itself accounts for around 20–30% of NPP, but such autocorrelation would tend to enhance the likelihood of finding apparently significant relationships, where in fact none are found.

Both within the intensive and wider plot data sets, woody biomass residence time does not vary strongly as a function of MCWD among the western sites, whereas it varies considerably in the eastern sites (Fig. 3e). While residence time is low (around 30–50 years) in the western sites, the eastern sites demonstrates high residence times at moderate MCWD (around 80–120 years at –200 mm). The patterns observed are consistent both within and among countries (Fig. S4). Plots in Venezuela and Colombia were excluded due to lack of clarity as to their edaphic position in western or eastern Amazonia.

The pattern in residence time is reflected in the patterns of above-ground biomass (Fig. 3f). Biomass is lowest in the driest sites, around 60–80 Mg C ha⁻¹, because residence times are so low. It rises moderately in western Amazonia (around 100–150 Mg C ha⁻¹ at MCWD = –200 mm) because residence times increase, but shows no trend between the moderately seasonal and aseasonal sites. In eastern Amazonia, it rises more substantially to a peak of 170–220 Mg C ha⁻¹ at MCWD = –200 mm, with some hint of a slight decline at less seasonal sites, consistent with the trend in residence time. Due to the strong effect of residence time, there are no significant relationships between above-ground biomass and GPP, NPP or woody growth (Fig. S5). The spatial variation in biomass is dominated by

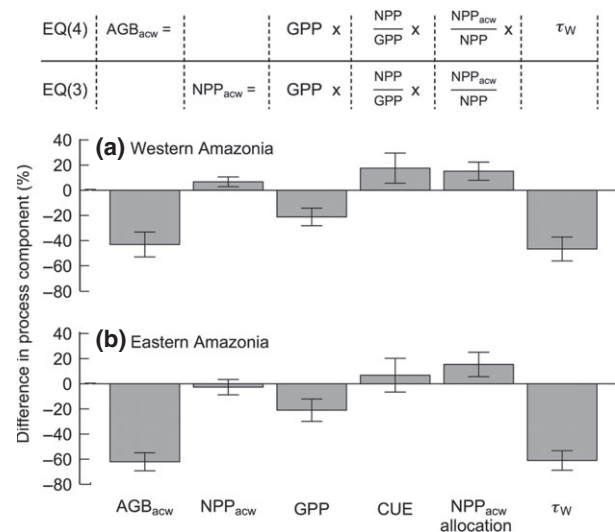


Fig. 6 Results from analysis framework exploring how above-ground woody growth varies between dry and wet forests. Bars indicate proportion difference (± 1 SE) in various productivity and carbon budget terms between the driest site and the mean of the wetter sites for the (a) western and (b) eastern sites.

the spatial variation in residence times (mortality rates), whereas GPP, NPP and woody growth rates have negligible influence on biomass.

Results from analysis framework for above-ground growth and biomass

In the western sites, there is no significant difference in mean woody productivity between the dry plots (Kenia) and the humid plots (Allpahuayo and Tambopata) (Fig. 6a). There is a significant ($21 \pm 7\%$; z -test, $P = 0.001$) decline in GPP in the dry plots, probably associated with the decline in leaf area and increased stomatal closure that was directly observed at the dry site in the dry season (Araujo-Murakami *et al.*, 2014). However, this decline is offset by the higher CUE ($+18 \pm 12\%$; $P = 0.07$) of the drier sites, and by increased allocation of NPP to stem growth ($+15 \pm 7\%$; $P = 0.02$), leading to a slight overall increase in woody growth at the dry sites ($+7 \pm 4\%$; $P = 0.06$).

A very similar pattern is observed for the eastern sites comparing the dry Tanguro plots relative to more humid Caxiuanã plots, with a $21 \pm 9\%$ ($P = 0.009$) decline in GPP at the drier site offset by an increase in woody allocation ($+15 \pm 10\%$; $P = 0.06$) and a nonsignificant increase in CUE ($+7 \pm 13\%$; $P = 0.3$), resulting in no significant difference in stem growth between the sites ($-3 \pm 6\%$; $P = 0.3$; Fig. 6b). In the eastern sites, the increase in allocation to stem growth (at the expense of branch turnover – see Fig. 3e, g) appears more important than the increase in CUE.

In both the eastern and the western sites, the clear decline in GPP in the drier sites is completely offset by shifts in CUE and allocation, resulting in either no decline, or even a net increase, in tree woody growth from wet to dry sites. Hence, the compensatory shifts in CUE and allocation effectively decouple spatial variations in GPP, NPP and wood growth.

Woody biomass is substantially lower at the dry sites in both seasonal water deficit gradients ($43 \pm 10\%$ lower in the west, $62 \pm 7\%$ lower in the east; $P < 10^{-5}$), but this decline is overwhelmingly explained by the strong decrease (approximate halving; $47 \pm 10\%$ in west, $61 \pm 8\%$ in east; $P < 10^{-5}$) of woody biomass residence time at the dry sites in both gradients (Fig. 6).

Discussion

This study presents the largest data set assembled to date that provides a comprehensive analysis of the productivity and autotrophic carbon cycling of lowland tropical forests, with ten plots covering geographical, hydrological and edaphic contrasts in Amazonia. Previous analyses have explored patterns of NPP allocation (Aragão *et al.*, 2009; Malhi *et al.*, 2011) and residence time in tropical forests (Galbraith *et al.*, 2013). A particular contribution of this new synthesis is the ability to evaluate GPP and CUE in relation to other carbon cycle components. Hence, we focus our discussion on the novel insights that quantification of GPP and CUE brings to our understanding of the carbon cycle. We highlight four emergent results, in the context of the autotrophic carbon budget framework presented in Fig. 1:

To what extent can key carbon budget parameters be predicted from precipitation and soils?

Our results suggest that annual GPP increases linearly as seasonal water deficit decreases, with similar relationships in the contrasting soils of eastern and western Amazonia. This is likely related to the duration and intensity of the reduction of photosynthesis in the dry season, either through closure of stomata or by the shedding of leaves in deciduous or semi-deciduous trees (del Aguila-Pasquel *et al.*, 2014; Araujo-Murakami *et al.*, 2014). CO₂ flux tower data show clear reduction of photosynthesis in the dry season in the southern fringe of Amazonia, but little limitation in forests with modest seasonal water deficits (Restrepo-Coupe *et al.*, 2013). These findings suggest it may be relatively straightforward to predict and model tropical forest GPP as a function of seasonality, irrespective of soil regime.

In contrast, we see no other strong relationships of other carbon cycling parameters as a function of sea-

sonal water deficit. Surprisingly, we also do not find a significant effect of soil properties, although it is possible that a larger data set would find a significant result. There is evidence that woody productivity is higher on the more fertile, less well-structured soils of western Amazonia (Malhi *et al.*, 2004; Quesada *et al.*, 2012), although this east–west gradient diminishes when the lower stature of western Amazonian trees is taken into account (Feldpausch *et al.*, 2012). Our findings on NPP allocation have the benefit of complete methodological consistency across sites, but are consistent with larger pan-tropical data sets (Malhi *et al.*, 2011), which have also demonstrated that woody growth shows little relationship to total NPP, whereas litterfall is a good predictor of total NPP. Our data on fine root production, which is rarely measured in the context of total NPP, also hint at a surprising, positive correlation between fine root production and total NPP (Fig. 5).

Can NPP or woody growth be reliably predicted from GPP, and vice versa?

Our findings show that GPP has only moderate power as a predictor of the variation in NPP across Amazonia and very little power as a predictor of woody biomass production, due to equally important variations in CUE and NPP allocation that are rarely quantified in ecosystem carbon cycle studies. This observation has ramifications for attempts to either determine and map tropical forest NPP from satellite data (e.g. the MODIS NPP product; Running *et al.*, 2004) or relate spatial or temporal changes in GPP to changes in tree growth rates. Until we have an improved understanding of the factors determining CUE and NPP allocation in tropical forests, such attempts have to be interpreted with caution.

The reason CUE varies between sites may be linked to life-history dynamics and the resource-economics spectrum: at more dynamic sites, the tree community is dominated by faster growing species that prioritize growth over defence and are also (on average) at a younger life stage with lower biomass and maintenance respiration costs. More conservative, defensive strategies found in less dynamic forests may carry high respiration costs associated with the production and maintenance of defence compounds (Coley *et al.*, 1985). This may also help explain why tropical forests appear to have lower CUE than many temperate forests (DeLucia *et al.*, 2007), which are often at a stage of vigorous recovery after disturbance or management.

In addition, our lack of quantification of below-ground exudate and mycorrhizae-associated fluxes may partially explain apparent trends in NPP and CUE. If these missing fluxes are larger on nutrient-poor

soils, this may be at the expense of other, more visible components of NPP and result in a decrease of apparent CUE (or BPE) on nutrient-poor soils (Vicca *et al.*, 2012). Examination of Fig. 4a suggests that such missing fluxes would need differ by as much as 2–4 Mg C ha⁻¹ yr⁻¹ between sites to account for all spatial differences in CUE. The plausibility of these fluxes will be explored in a forthcoming paper (C.E. Doughty, unpublished results), but it seems possible that such terms may provide a partial (but not complete) explanation of differences in CUE between sites.

What is the relative importance of different aspects of the carbon budget (GPP, CUE, NPP allocation and residence time) in determining spatial variation in biomass in Amazonian tropical forests?

Our analyses show that spatial variation in biomass is overwhelmingly determined by variation in residence time. GPP, NPP and woody growth are all poor predictors of Amazonian forest biomass (Fig. 3, Fig. S5). This has been noted in our previous work in Amazonia (e.g. Baker *et al.*, 2004; Malhi *et al.*, 2006; Delbart *et al.*, 2010; Castanho *et al.*, 2013); however, the analysis here advances on this by providing a quantitative comparison with other aspects of the carbon budget such as GPP. It also shows the consistent, but divergent, relationships between residence times and water deficit in eastern and western Amazonia and in particular, the low residence time 'hyperdynamic' belt around the southern dry fringe of Amazonia (Marimon *et al.*, 2014). If we are to develop a predictive understanding of the spatial variation of biomass in old-growth forests, it is probably a higher priority to understand the determinants of mortality rates and residence times, rather than the determinants of GPP and NPP. This may also have implications for predicting the future behaviour of the biosphere carbon sink – if rising atmospheric CO₂ stimulates GPP, would this be manifest primarily as an increase in biomass, or an increase in turnover rates (Malhi, 2012)? At the driest sites (Tanguro and Kenia), it is possible that our estimates of residence time are biased downwards if the forests are still far from biomass equilibrium following fire disturbance. However, both sites show a mixed-age structure and little net biomass increase over time, suggesting that they are not in a strong secondary stage and any such bias is likely to be small. The short residence times at the dry margin reported here are consistent with the high stem turnover rates reported at other southern Amazonian sites (Marimon *et al.*, 2014) and therefore likely reflect a genuine phenomenon.

Why do biomass residence times, which are mainly dominated by the mortality rates of medium and large trees, vary so much across Amazonia? Understanding the determinants of tree death is a major question in

forest ecology (Stephenson *et al.*, 2011); explanations must account for both intrinsic mortality rates (e.g. self-thinning in a light-limited and resource-limited system, interacting with life-history trade-offs across species) and the role of exogenous disturbances (e.g. blow-downs). The strong contrast between east and west Amazonia is almost certainly linked to soil substrate, whether through higher fertility driving resource demanding, high mortality strategies, or the weaker soil structure driving higher tree fall rates (Quesada *et al.*, 2012). The short residence times at the dry fringe may be driven by drought-associated mortality, which also end up favouring high growth, short lifetime strategies.

Are the relatively low values of biomass in seasonally dry tropical forests caused by a decrease in GPP and woody growth rates, or an increase in mortality rates?

Our results show that the seasonally dry tropical forests studied here have low biomass because they are dynamic, not because they are unproductive. Biomass is lower at the dry sites in both seasonal water-deficit gradients, despite little decline in stem productivity (Fig. 6). The dry plots have low biomass not because they have lower growth rates (they do not) or lower GPP (they do, but this is completely offset by increases in CUE and/or woody allocation), but because the trees in these plots have shorter lifetimes and die more quickly. Mortality rates (i.e. residence times) overwhelmingly explain spatial variation in biomass in these plots, photosynthesis or growth do not. Again, there may be a direct link between the high mortality rates and the high CUE and/or woody allocation; such a dynamic system may favour trees with inherently shorter life-history strategies, an early mean life stage and less investment in defence. Understanding the role of mortality and turnover in determining the structure of dry forests is an important and neglected component in understanding their response to atmospheric change.

In conclusion, this study demonstrates the critical importance of considering the various components of ecosystem forest carbon budgets, particularly carbon use efficiency and residence time, if we are to understand relationships between photosynthesis, growth, allocation and biomass, and the spatial variation of these parameters (Landsberg & Sands, 2010; Pan *et al.*, 2013). We focussed on a unique data set of ten lowland Amazonian plots where we conducted a comprehensive quantification of the carbon cycle (Malhi *et al.*, 2009); however, the insights gained are probably equally applicable for other forest and woodland ecosystems, and particularly so in other tropical forest regions. These ten plots provide substantial new insights and represent a major data collection effort, but are clearly not sufficient

in and of themselves to untangle the spatial variability of links between GPP, growth and biomass. Further plots are needed across the tropics engaging a standardized protocol, something that is being attempted by the GEM network. Moreover, an important next step will be to employ data from these and other new sites to develop and test hypotheses and models for how GPP, autotrophic respiration, allocation and residence time respond to varying environmental conditions.

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Supporting Information

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

Figure S1. Relationship between two approaches for estimating gross primary productivity.

Figure S2. Relationships among components of the carbon cycle and annual precipitation.

Figure S3. Relationships among components of net primary productivity and seasonal water deficit.

Figure S4. Relationship between residence time and above-ground biomass and seasonal water deficit.

Figure S5. Relationship between above-ground biomass and various components of the carbon cycle.

Table S1. Sampling period and interval for data collection in 1 ha plots.

Table S2. Comparison of approaches for estimating gross primary productivity.

Table S3. Measurements of carbon cycle components measured in 1 ha plots.

Appendix S1. Detailed data collection methods for 1 ha plots.