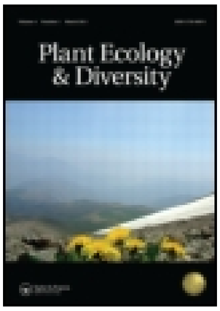

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The seasonal cycle of productivity, metabolism and carbon dynamics in a wet aseasonal forest in north-west Amazonia (Iquitos, Peru)

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The seasonal cycle of productivity, metabolism and carbon dynamics in a wet aseasonal forest in north-west Amazonia (Iquitos, Peru)

Jhon del Aguila-Pasquel[a,b], Christopher E. Doughty[c]*, Daniel B. Metcalfe[d], Javier E. Silva-Espejo[e], Cecile A.J. Girardin[c], Jack A. Chung Gutierrez[b], Gilberto E. Navarro-Aguilar[a], Carlos A. Quesada[f], Carlos G. Hidalgo[a], Jose M. Reyna Huaymacari[a], Kate Halladay[c], Dennis del Castillo Torres[b], Oliver Phillips[g] and Yadvinder Malhi[c]*

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Background: The forests of north-west Amazonia are characterised by the highest levels of tree diversity in the world, high rainfall and relatively fertile soils.
Aims: Here we present a comprehensive description of the carbon cycle of two 1 ha forests plots in Allpahuayo, near Iquitos, Peru, one on an occasionally inundated alisol/gleysol landscape, the other on an arenosol (sandy soil).
Methods: Data on the components of net primary productivity (NPP) and autotrophic respiration were collected over the period 2009–2011, and summed to estimate gross primary productivity (GPP) and carbon use efficiency (CUE).
Results: Overall, these forests showed high values of GPP (39.05 ± 4.59 and 41.88 ± 4.60 Mg C ha^{-1} year^{-1}). Despite the lack of a dry season, the forests showed distinct seasonality in tree growth, litterfall, flowering and fine root productivity. This showed that tropical forests with little seasonality in water supply can still exhibit distinct seasonality in NPP and carbon use, apparently synchronised to the solar radiation cycle. We found remarkably little difference in productivity between the alisol/gleysol plot and the arenosol plot.
Conclusions: The GPP was higher than those reported for forests in Brazilian Amazonia on more infertile soils. The CUE was also higher, which may be related to the high forest dynamism and natural disturbance rate. These two factors combined to result in amongst the highest NPP values reported for Amazonia.

Keywords: CUE; GPP; NPP; respiration; spatial variation; tropical forests; white sand soil

Introduction

The tropical forests of north-western Amazonia can provide an interesting contrast to better studied eastern Amazonian forests. Several eastern Amazonian rain forests have had detailed full carbon cycle analyses (Malhi et al. 2009; Metcalfe et al. 2010). However, there is much less detailed knowledge about tropical forests that do not generally experience a dry season, such as those in north-eastern Peru. This region generally does not have any months during the year where rainfall is below 100 mm month^{-1}. Most tropical forests have monthly evapotranspiration rates of ~100 mm month^{-1} (Fisher et al. 2009), and hence there is likely to be little drought stress in normal years in this region. Tropical forests with little to no dry season occupy a large portion of the western Amazon, and it is therefore important to understand how future climate change may impact their carbon stocks. An accurate understanding of the factors influencing tropical forest growth and seasonality is important because they are productive ecosystems that account for about one-third of net primary production (NPP) globally (Field et al. 1995).

In addition to climate, variation in soil type has been found to greatly influence the composition and dynamics of Amazonian forests (Quesada et al. 2011). Even along short distances there can be large changes in soil fertility, soil physical properties and water budget that can affect forest dynamics, and there are few datasets comparing such effects on carbon cycling.

There has been recent effort to study a wider range of the very diverse Amazon forest types (Malhi et al. 2002). However, most of the focus has been on aboveground biomass (Malhi et al. 2006), woody production (Malhi et al. 2004), and litterfall (Chave et al. 2010) as individual components of NPP. A recent review of allocation of NPP in tropical forests has shown that allocation patterns were fairly consistent across sites, and suggested that allocation to canopy was fairly invariant, with the main variation occurring as a shift in allocation between fine roots and woody tissue (Malhi et al. 2011). Beyond biomass and biomass change, there has been much less focus on other equally important aspects of the carbon cycle, such as gross primary productivity (GPP), autotrophic respiration and carbon use efficiency (CUE).

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An important question in ecosystem ecology is: how much carbon is allocated above ground versus below ground? Below-ground carbon allocation might, or might not, vary as a function of soil type. One conceptual model (Litton and Giardina 2008) predicted that as mean annual temperatures increased, carbon allocated below ground would increase because as the temperature constraint was reduced, trees would invest more below ground to reduce resource supply limitations. The warm wet conditions of the Peruvian Amazon provide an area to test this theory.

CUE is the ratio of NPP to GPP, or the fraction of fixed carbon that is allocated to new tissue structures (e.g. leaves, wood and fine roots). There are very few data on CUE, especially in tropical forests. For old-growth forests in eastern Amazonia, CUE has been estimated to be around 0.3 (Chambers et al. 2004;Malhi et al. 2009), with values up to 0.49 in a forest after disturbance (Malhi et al. 2009). There is evidence that CUE may decrease with sustained drought (Metcalfe et al. 2010).

In this paper, we extend the small body of existing tropical forest NPP and autotrophic respiration data by reporting results from two 1 ha plots in the lowland Amazonian forests of north-eastern Peru, in western Amazonia. Western Amazonia has been shown to generally have higher productivity than the sites in eastern Amazonia that were reported by Malhi et al. (2009), a difference that has been ascribed to soil fertility, particularly phosphorus availability (Malhi et al. 2004; Aragao et al. 2009; Quesada et al. 2010) rather than to climate, or possibly also to the markedly different physical conditions of soils across Amazonia (Quesada et al. 2011).

We compared the cycling and allocation of carbon in two plots (<1 km apart) with contrasting soils, one a forest on a mainly white sand substrate with relatively low species richness (Alp C) and the other on a sloping, mainly clay substrate with greater species richness (Alp A). We show the results of 2 years of detailed annually averaged and seasonal carbon cycling measurements. We asked the following specific questions:

1. How does the lack of a dry season affect the seasonality of NPP, and the absolute magnitude of GPP and NPP?
2. How does carbon cycling differ in these forests between the white sand and the clay soils?

Materials and methods

Site characteristics

The study site was situated ~25 km south of the city of Iquitos, Maynas Province, Department of Loreto, Peru, within the Allpahuayo-Mishana National Reserve (3° 57’ S, 73° 26’ W) that is administered by the Peruvian Institute for Amazonian Research (IIAP). The altitude above sea level in the Reserve varies between 110 and 180 m. Soils vary in texture from clay to almost pure sand, and in drainage from waterlogged swamps to well-drained hill tops (Vormisto et al. 2000).

Two 1 ha (Alp A: 20 m × 500 m and Alp C: 40 m × 250 m) research plots were established within the RAINFOR network of long-term forest inventory plots (Malhi et al. 2002), in 1990 and 2001. These represent a contrasting pair of the 15 plots in the Iquitos area within the RAINFOR network that have been monitored for tree species composition and biomass since the early 1980s (Gentry 1988). Plot Alp A is a forest with low-lying areas that are occasionally waterlogged and higher areas that are better drained. Both sites are undulating (Alp A: mean slope 1.4%, maximum 5%; Alp C mean slope 2.7%, maximum 17.5%). The soil in the occasionally flooded parts of Alp A is haplic gleysol (alumnic, hyperdistic). The vegetation of plot Alp C is situated on a very sandy hyperdistic haplic arenosol (Quesada et al. 2010) with very good drainage. All soils were classified by Quesada et al. (2010) according to the recent World Reference Base for Soil Resources – (IUSS Working Group WRB, 2006) (Quesada et al 2010). Alp A corresponds to the RAINFOR codes Alp-11 (the gleysol parts) and Alp-12 (the alisol parts). Alp C corresponds to the RAINFOR plot code Alp-30.

Alp C sands probably had a similar origin to the sands occurring on the gleysol part of Alp A, but in the case of Alp C, the higher position on the landscape and good drainage resulted in large differences in weathering which probably explains the current soil differences. Readily available P pools were very similar between the two plots at Alp A and Alp C (see Table 3, Results section), while the extractable P, which is essentially the biologically active pool (P_{Total} – residual), was higher at Alp A, and lower at Alp C. Therefore, although there was virtually no difference in readily available P content between the plots, the phosphorus capital of Alp A was higher.

In plot Alp A there were 184 tree species ≥10 cm DBH (diameter at breast height), including palms and vines, distributed in 131 genera and 47 families. The most common genera were *Eschweilera* (Lecythidaceae), *Guatteria* (Annonaceae), *Inga* (Fabaceae), *Iryanthera* (Myristicaceae), *Ocotea* (Lauraceae), *Pouteria* (Sapotaceae), *Protium* (Burseraceae) and *Sloanea* (Elaeocarpaceae). There was a dense understory with ferns, abundant shrubs and large grasses. Plot Alp A had higher species richness with lower number of individuals per species than Alp C.

Plot Alp C had 99 tree species ≥10 cm DBH, including palms and vines, distributed in 65 genera and 37 families (Zárate et al. 2006). The dominant species included *Anaxagorea brachycarpa* (Annonaceae), *Caraipa utilis* (Clusiaceae), *Dendropanax umbellatus* (Araliaceae), *Dicymbe uaiparuensis* (Fabaceae), *Euterpe catinga* (Arecaceae), *Neea macrophylla* (Nyctaginaceae), *Oxandra euneura* (Annonaceae), *Pachira brevipes* (Malvaceae), *Sloanea spathulata* (Elaeocarpaceae), *Ternstroemia klugiana* (Ternstroemiaceae), and *Tovomita calophyllophylla* (Clusiaceae).

Carbon fluxes

The protocols used to estimate ecosystem C flux components within the 1 ha plot (divided into 25 20 m × 20 m subplots) were largely based on those developed by the RAINFOR–GEM network. Measurements were distributed evenly through the plot, approximately one per subplot (except for ingrowth cores, which at $N = 16$, were at the corners of subplots). A detailed description is available online for download (http://gem.tropicalforests.ox.ac.uk) and in the online supplemental material accompanying this paper. Summaries of the different components quantified, and the field methods and data processing techniques used are presented in Tables 1 and 2, respectively. We calculated above- and below-ground *NPP*, NPP_{AG} and NPP_{BG}, respectively, using the following equations:

$$NPP_{\mathrm{AG}} = NPP_{\mathrm{ACW}} + NPP_{\mathrm{litter\ fall}} + NPP_{\mathrm{branch\ turnover}} + NPP_{\mathrm{herbivory}} \quad (1)$$

$$NPP_{\mathrm{BG}} = NPP_{\mathrm{fine\ roots}} + NPP_{\mathrm{coarse\ roots}} \quad (2)$$

This neglects several small *NPP* terms, such as *NPP* lost as volatile organic emissions or litter decomposed in the canopy. Total R_{a} is estimated as:

$$R_{\mathrm{a}} = R_{\mathrm{leaves}} + R_{\mathrm{stems}} + R_{\mathrm{rhizosphere}} \quad (3)$$

Here we count root exudates and transfer to mycorrhizae as a portion of $R_{\mathrm{Rhizosphere}}$ rather than as *NPP*. In quasi-steady state conditions (and on annual timescales or longer where there no net change in plant non-structural carbohydrate storage), *GPP* should be approximately equal to the sum of *NPP* and $R_{\mathrm{a.}}$ Hence, we estimated GPP as:

$$GPP = NPP_{\mathrm{AG}} + NPP_{\mathrm{BG}} + R_{\mathrm{a}} \quad (4)$$

We estimated the *CUE* as the proportion of total *NPP* divided by *GPP*:

$$CUE = (NPP_{\mathrm{AG}} + NPP_{\mathrm{BG}})/(NPP_{\mathrm{AG}} + NPP_{\mathrm{BG}} + R_{\mathrm{a}}) \quad (5)$$

Meteorological data

Solar radiation, air temperature, relative humidity and precipitation data were collected from an automatic weather station (AWS) (Skye Instruments, Llandrindod, UK) at an open site about 1 km from the plot (detailed meteorological methodology in the supplementary online material). Soil moisture content in the top 18 cm was measured monthly at 25 locations per plot using a Hydrosense probe (Campbell Scientific Ltd., Loughborough, UK).

Statistics and error analysis

An important consideration was the assignment and propagation of uncertainty in our measurements. There were two primary types of uncertainty. Firstly, there was sampling uncertainty associated with the spatial heterogeneity of the study plot and the limited number of samples. Examples include the variability among litter traps, or among fine root ingrowth cores. Secondly, there was a systematic uncertainty associated with either unknown biases in measurement, or uncertainties in scaling measurements to the plot level. Examples of unknown biases included the possibility of soil CO_2 in the transpiration stream affecting the stem and CO_2 efflux measurements, and uncertainties in scaling included the allometry of scaling of bole stem CO_2 efflux to whole-tree stem respiration, or leaf dark respiration to whole-canopy dark respiration. Here we assumed that most *NPP* terms were measured fairly precisely and sampled without large biases: hence the *NPP* component measurements were dominated by sampling uncertainty, which can be reliably, estimated assuming a normal distribution. On the other hand, some of the main autotrophic respiration terms were probably dominated by systematic uncertainty. This systematic uncertainty can be very hard to reliably quantify; here in each case we made an explicit and conservative estimate of the systematic uncertainty of key variables. Our assumptions about the uncertainty in each measurement are clearly presented in the results (see Table 3).

Repeated-measures analysis of variance (ANOVA) was used to test for significant seasonal shifts in ecosystem carbon components between plots. In addition, a Student's *t*-test assessed mean annual differences between the two plots. All estimated fluxes reported in this study are in Mg C ha^{-1} year^{-1}, and all reported errors show ±1 SE. Error propagation was carried out for all combination quantities using standard rules of quadrature, assuming that uncertainties are independent and normally distributed.

Results

Meteorology

The site had less seasonality in rainfall than other Amazonian forests, ranging from over 300 mm month^{-1} at the peak of the rainy season to slightly above 100 mm month^{-1}, and there was no dry season. There was strong seasonality in solar radiation, with higher values from July to December. There was little seasonality in air temperature or relative humidity, although there was a slight peak that matched the increased solar radiation. The mean annual rainfall over the 3-year period was approximately 2689 mm and the mean annual air temperature was ca. 25.2 °C. Soil moisture content (top 18 cm) was much higher at the clay site at Alp A (26.8 ± 0.34%) than the sandy site in Alp C (10.8 ± 0.22% water) (Figure 1).

Table 1. Methods for intensive studying of carbon dynamics in Allpahuayo-Mishana National Reserve, near the city of Iquitos, Maynas Province, Department of Loreto, Peru (see also supplementary material and RAINFOR-GEM manual 2012).

	Component	Description	Sampling period	Sampling interval
Above-ground net primary productivity (NPP_{AG})	Above-ground coarse wood net primary productivity (NPP_{ACW})	Forest inventory: All trees ≥10 cm DBH censused to determine growth rate of existing surviving trees and rate of recruitment of new trees. Stem biomass calculated using the Chave et al. (2005) allometric equation for tropical moist forests, employing diameter, height and wood density data. Six 20 m × 20 m subplots were established to carry out censuses on small trees (2–10 cm DBH) using calipers and data was scaled up to one hectare.	2005–2011 >10 cm 2010–2011 <10 cm	Every year (trees ≥10 cm DBH) Every year (trees 2–10 cm DBH)
		Seasonal growth: Dendrometers were installed on all trees >10 cm DBH in each plot to determine the spatial-temporal and seasonal variation in growth.	April 2009–June 2011	Every three months
	Branch turnover net primary productivity ($NPP_{\text{branch turnover}}$)	Branches (excluding those fallen from dead trees) were surveyed within one 1 m by 500 m transect at Alp A and one 1 m by 250 m transect at Alp C; small branches were cut to include only the transect-crossing component, removed and weighed. Larger branches had their dimensions taken (diameter at 2 points) and all were assigned a wood density value according to their decomposition class.	November 2009–September 2010	Every three months
	Litterfall net primary productivity ($NPP_{\text{litterfall}}$)	Litterfall production of dead organic material less than 2 cm diameter was estimated by collecting litterfall in 0.25 m^2 (50 × 50 cm^2) litter traps placed at 1 m above the ground at the centre of each of the 25 subplots in each plot.	January 2009–April 2011	Every 15 days
	Leaf area index (LAI)	Canopy images were recorded with a digital camera and hemispherical lens near the centre of each of the 25 subplots in each plot, at a standard height of 1 m, and during overcast conditions (Demarez et al. 2008). LAI was estimated from these images using CAN-EYE software.	August 2010–July 2011	Every month
	Loss to leaf herbivory ($NPP_{\text{herbivory}}$)	We employed data on the fraction of canopy leaf area that is lost to herbivory (18.8 ± 1.3%) collected from two forest plots in Tambopata, Madre de Dios, SE Peru, plots with similar carbon cycle properties to the site reported here. We multiplied this fractional herbivory with the annual leaf litterfall measured here (Table 2) to estimate total herbivory.	n/a	Not directly measured
Below-ground net primary productivity (NPP_{BG})	Coarse root net primary productivity ($NPP_{\text{coarse roots}}$)	This component of productivity was not measured directly and was estimated by assuming that coarse root productivity was 0.20 ± 0.03 of above-ground woody productivity, based on published values of the ratio of coarse root biomass to above-ground biomass (Jackson et al. 1996, Cairns et al. 1997).	n/a	Not directly measured
	Fine root net primary productivity ($NPP_{\text{fine roots}}$)	Sixteen ingrowth cores (mesh cages 14 cm diameter, installed to 30 cm depth) were installed in each plot. Cores were extracted and roots were manually removed from the soil samples in four 10 min time steps and the pattern of cumulative extraction over time was used to predict root extraction beyond 40 mins. Root-free soil was then re-inserted into the ingrowth core. Collected roots were thoroughly rinsed, oven dried at 80°C, and weighed.	March 2010–September 2011	Every three months

(*Continued*)

Table 1. (*Continued*).

	Component	Description	Sampling period	Sampling interval
Autotrophic and heterotrophic respiration	Total soil CO_2 efflux (R_{soil})	Total soil CO_2 efflux was measured using a closed dynamic chamber method, at the centre of each of the 25 subplots in each plot with an infra-red gas analyzer (IRGA; EGM-4) and soil respiration chamber (SRC-1) sealed to a permanent collar in the soil.	June 2009–September 2011	Every month
	Soil CO_2 efflux partitioned into autotrophic ($R_{rhizosphere}$) and heterotrophic ($R_{soilhet}$) components	At four points at each corner of the plot, we placed plastic tubes of 10 cm diameter; three tubes with short collars (10 cm depth) allowing both heterotrophic and rhizosphere respiration, three tubes with longer collars (40 cm depth) with no windows to exclude both roots and mycorrhizae and three tubes with fine mesh to exclude fine roots but include mycorrhizae. The sets of three have a different litter layer treatment (normal litter, no litter, double litter). At the centre of each plot, a control experiment was carried out in order to assess the effects of root severing and soil structure disturbance that occurs during installation.	June 2009–September 2011	Every month
	Canopy respiration (R_{leaves})	In each plot, leaf dark respiration and photosynthesis at PAR levels of 1000 µmol m^{-2} s^{-1} were recorded for 20 trees with an IRGA and specialized cuvette. For each tree, we randomly selected one branch each from sunlit and shaded portions of the canopy and immediately re-cut the branches underwater to restore hydraulic connectivity (Reich et al., 1998).	November 2010	Once
	Above-ground live wood respiration (R_{stems})	Bole respiration was measured using a closed dynamic chamber method, from 25 trees distributed evenly throughout each plot at roughly 1.3 m height with an IRGA (EGM-4) and soil respiration chamber (SRC-1) connected to a permanent collar, sealed to the tree bole surface.	March 2010–September 2011	Every month
	Coarse root respiration ($R_{coarse\ roots}$)	This component of respiration was not measured directly and was estimated by multiplying estimated above-ground live wood respiration by 0.20 (same ratio used in this study to estimate coarse root biomass and growth – see above).	n/a	Not directly measured

Woody NPP

Wood density weighted by mean basal area for Alp A was 0.63 and 0.65 g cm^{-3} for Alp C. Mean small tree height (<20 cm DBH) was 14.6 ± 4.6 m for Alp A and 15.9 ± 1.5 m for Alp C, mean medium tree height (>20 and <40 cm DBH) was 20.6 ± 5.6 m for Alp A and 21.6 ± 2.1 m for Alp C, and mean large tree height (>40 cm DBH) was 29.2 ± 6.7 m for Alp A and 28.8 ± 3.4 m for Alp C. Total stand-level above-ground biomass at Alp A for all trees (>10 cm DBH) was 141.76 Mg C ha^{-1} and 90.98 Mg C ha^{-1} at Alp C. Stem density (>10 cm DBH) was 576 stems ha^{-1} for Alp A and 476 stems ha^{-1} for Alp C. Alp A had 31 palms (>10 cm DBH) whose biomass we estimate to be 4.3 Mg C ha^{-1} with a NPP of 0.28 ± 0.08 Mg C ha^{-1} $year^{-1}$. Total stand-level above-ground biomass for trees (<10 cm DBH) was 8.84 Mg C ha^{-1} at Alp A and 5.3 Mg C ha^{-1} at Alp C. Stem density (<10 cm DBH) was 5325 stems ha^{-1} for Alp A and 4225 stems ha^{-1} for Alp C. Therefore, total stand-level above-ground biomass (for 2010) at Alp A was 150.60 Mg C ha^{-1} and 96.28 Mg C ha^{-1} for Alp C.

Over 6 years 2005–2011 (tree productivity was measured for a longer period than the rest of the measurements), we calculated the mean above-ground wood productivity of stems ≥10 cm DBH to be 3.45 ± 0.35 Mg C ha^{-1} $year^{-1}$ for Alp A and 2.73 ± 0.27 Mg C ha^{-1} $year^{-1}$ for Alp C. Small tree NPP (<10 cm DBH) was measured between 2010 and 2011 and was 0.85 ± 0.09 Mg C ha^{-1} $year^{-1}$ at Alp A and 0.21 ± 0.02 Mg C ha^{-1} $year^{-1}$ at Alp C. There was a slight seasonality to woody NPP with a peak in woody growth in December with 0.36 Mg C ha^{-1} $month^{-1}$ and a minimum in woody growth

Table 2. Data analysis techniques for intensive studying of carbon dynamics in Allpahuayo-Mishana National Reserve, near the city of Iquitos, Maynas Province, Department of Loreto, Peru (see also online supplemental material and RAINFOR-GEM manual 2012).

Component		Data processing details
Above-ground net primary productivity (NPP_{AG})	Above-ground coarse wood net primary productivity (NPP_{ACW})	Biomass calculated using the Chave et al. (2005) allometric equation for tropical moist forests: $AGB = 0.0509 \times (\rho D^2 H)$ where AGB is above-ground biomass (kg), ρ is density (g cm^{-3}) of wood, D is DBH (cm) and H is height (m). To convert biomass values into carbon, we assumed that dry stem biomass is 47.3% carbon (Martin and Thomas 2011). Where height data were not available, it was estimated by applying the allometric equation of Feldpausch et al. (2011).
	Branch turnover net primary productivity ($NPP_{\mathrm{branch\ turnover}}$)	See RAINFOR-GEM manual (Version 2.2, 2012, p.61) for description.
	Litterfall net primary productivity ($NPP_{\mathrm{litterfall}}$)	$NPP_{\mathrm{litterfall}}$ is calculated as follows: $NPP_{\mathrm{litterfall}} = NPP_{\mathrm{canopy}}$ – loss to leaf herbivory. Litterfall is separated into different components, oven dried at 80 °C to constant mass and weighed. Litter is estimated to be 53.2% carbon (S. Patiño, unpublished analysis).
	Leaf area index (LAI)	LAI estimated using 'true LAI' output from the programs which account for clumping of foliage, and assuming a fixed leaf inclination angle of 49.6°, based on average estimates. Leaves were separated into sunlit and shaded fractions using the following equation: $F_{\mathrm{sunlit}} = (1 - \exp(-K^{*}\mathrm{LAI}))/K$, where K is the light extinction coefficient, and F_{sunlit} is the sunlit leaf fraction (Doughty and Goulden 2008). The model assumptions are randomly distributed leaves, and $K = 0.5/\cos(Z)$ where Z is the solar zenith angle, which was set to 30° in this study.
	Loss to leaf herbivory ($NPP_{\mathrm{herbivory}}$)	The fractional herbivory (H) for each leaf was then calculated as: $H = (A_{\mathrm{nh}} - A_{\mathrm{h}})\ /\ A_{\mathrm{nh}}$ where A_{h} is the area of each individual leaf including the damage incurred by herbivory and A_{nh} is the leaf area prior to herbivory. The average value of H of all leaves collected per litterfall trap was derived and plot level means were calculated.
Below-ground net primary productivity (NPP_{BG})	Coarse root net primary productivity ($NPP_{\mathrm{coarse\ roots}}$)	See RAINFOR-GEM manual (Version 2.2, 2012, p.47) for description and range of Root:shoot ratio.
	Fine root net primary productivity ($NPP_{\mathrm{fine\ roots}}$)	Roots were manually removed from the soil samples in four 10 min time steps, according to a method that corrects for underestimation of biomass of hard-to-extract roots (Metcalfe et al. 2007) and used to predict root extraction beyond 40 min (up to 100 min); we estimate that there was an additional 36.5% correction factor for fine roots not collected within 40 min. Correction for fine root productivity below 30 cm depth increased the value by 39%.
Autotrophic and heterotrophic respiration	Total soil CO_2 efflux (R_{soil})	Soil surface temperature (T260 probe, Testo Ltd, Hampshire, UK) and moisture (Hydrosense probe, Campbell Scientific Ltd, Loughborough, UK) were recorded at each point after efflux measurement.
	Soil CO_2 efflux partitioned into autotrophic ($R_{\mathrm{rhizosphere}}$) and heterotrophic (R_{soilhet}) components	The partitioning experiment allows estimation of the relative contributions of (1) roots, (2) mycorrhizae and (3) soil organic matter to total soil CO_2 efflux. Contributions are estimated from differences between collars subjected to different treatments, in excess of pre-existing spatial variation. In recognition of the substantial uncertainty in this estimate, we assigned a 10% error to the multiplying factor.
	Canopy respiration (R_{leaves})	To scale to whole-canopy respiration, mean dark respiration for shade and sunlit leaves were multiplied by the respective estimated fractions of total LAI. To account for daytime light inhibition of leaf dark respiration, we apply the inhibition factor applied in Malhi et al. (2009) (67% of daytime leaf dark respiration, 33% of total leaf dark respiration). In recognition of the substantial uncertainty in this estimate, we assigned a 30% error to the multiplying factor.
	Above-ground live wood respiration (R_{stems})	To estimate plot-level stem respiration tree respiration per unit bole area was multiplied by plot stem are index, estimated with the following equation (Chambers et al. 2004): $\log(SA) = -0.105 - 0.686\log(DBHb) + 2.208\log(DBHb)^2 - 0.627\log(DBHb)^3$ where H is tree height, and $DBHb$ is bole diameter at 1.3 m height. Finally, for all 25 trees together we regressed mean annual bole respiration against total annual growth. In recognition of the substantial uncertainty in this estimate, we assigned a 30% error to the multiplying factor.
	Coarse root respiration ($R_{\mathrm{coarse\ roots}}$)	In recognition of the substantial uncertainty in this estimate, we assigned a 50% error (±0.10) to the multiplying factor.

Table 3. Total yearly averaged canopy NPP, branch NPP, trunk NPP, coarse root NPP, fine root NPP, canopy respiration, wood respiration, rhizosphere respiration, coarse root respiration, total autotrophic respiration, soil heterotrophic respiration, soil respiration NPP, GPP and CUE for two 1-ha plots Alp A and Alp C plots, in the Allpahuayo-Mishana National Reserve, near the city of Iquitos, Maynas Province, Department of Loreto, Peru. Sample error is uncertainty associated with the spatial heterogeneity of the study plots and the limited number of samples. Total error is sampling error plus an estimate of systematic uncertainty associated with either unknown biases in measurement, or uncertainties in scaling measurements to the plot level.

	Alp A			Alp C		
	Mean	Sample error	Total error	Mean	Sample error	Total error
$NPP_{\text{litterfall}}$	4.20	0.85	0.85	5.66	0.80	0.80
NPP_{leaf}	2.68	0.66	0.66	4.05	0.56	0.56
NPP_{flower}	0.09	0.09	0.09	0.09	0.01	0.01
$NPP_{\text{ fruit}}$	0.29	0.20	0.20	0.31	0.15	0.15
$NPP_{\text{ twigs}}$	0.56	0.28	0.28	0.97	0.49	0.49
$NPP_{\text{herbivory}}$	0.50	0.12	0.12	0.76	0.11	0.11
$NPP_{\text{branch turnover}}$	1.42	0.14	0.14	1.01	0.10	0.10
$NPP_{\text{ACW} > \text{10cm dbh}}$	3.45	0.35	0.35	2.73	0.27	0.27
$NPP_{\text{ACW} < \text{10cm dbh}}$	0.85	0.09	0.09	0.21	0.02	0.02
$NPP_{\text{coarseroot}}$	0.69	0.07	0.07	0.55	0.05	0.05
NPP_{fineroot}	3.02	0.29	0.29	3.50	0.38	0.38
R_{canopy}	8.92	1.35	3.00	11.35	0.79	3.50
R_{stem}	9.63	0.99	3.05	8.11	0.77	2.55
$R_{\text{rhizosphere}}$	4.44	0.81	0.92	6.38	0.67	0.93
$R_{\text{coarseroot}}$	1.93	0.00	0.98	1.62	0.00	0.83
R_{soilhet}	13.69	2.25	2.64	11.80	1.57	1.97
R_{soil}	18.12	2.39	2.39	18.18	1.71	1.71
R_{a}	24.91	1.86	4.48	27.46	1.30	4.50
NPP	14.14	0.99	0.99	14.41	0.94	0.94
GPP	39.05	2.11	4.59	41.88	1.60	4.60
CUE	0.36	0.03	0.05	0.34	0.03	0.04

in June with 0.24 Mg C ha^{-1} month^{-1} for Alp A. Alp C showed a similar, but more extreme seasonal pattern with growth peaking in Dec at 0.33 Mg C ha^{-1} month^{-1} and a minimum in June 0.18 Mg C ha^{-1} month^{-1} (Figure 2). We estimated coarse root NPP as 20% of stem NPP and therefore 0.69 Mg C ha^{-1} year^{-1} for Alp A and 0.55 Mg C ha^{-1} year^{-1} for Alp C. Dividing the above-ground biomass by the above-ground wood biomass productivity, we estimated stem biomass residence times of 41 and 33 years for the two plots.

Canopy NPP

Leaf litter at Alp A averaged significantly ($P < 0.001$) less than Alp C. Twig NPP was not significantly different in Alp A than Alp C. There was no significant difference in reproductive litter (fruits and flowers) between Alp A and Alp C.

Total canopy NPP (including palm NPP for Alp A) was 4.70 ± 0.85 Mg C ha^{-1} year^{-1} at Alp A and 6.42 ± 0.80 Mg C ha^{-1} year^{-1} at Alp C (Table 3). Of this, leaves accounted for 2.68 ± 0.66 Mg C ha^{-1} year^{-1} at Alp A and 4.05 ± 0.56 Mg C ha^{-1} year^{-1} at Alp C. We estimated herbivory to be 0.50 ± 0.06 Mg C ha^{-1} year^{-1} at Alp A and 0.76 ± 0.11 Mg C ha^{-1} year^{-1} at Alp C, based on herbivory data from a site in south-eastern Peru (D.B. Metcalfe, pers. comm.).

Branch turnover

Total estimated annual branch turnover NPP averaged 1.42 Mg C ha^{-1} year^{-1} at Alp A and 1.01 Mg C ha^{-1} year^{-1} at Alp C (Figure 3).

Fine root NPP

We used the ingrowth core method to measure fine root growth for two 3 month intervals, April–June and June–September (data collection issues invalidated data collected at other times of the year so we are not able to report the seasonal cycle of fine root productivity). Total fine root growth for Alp A averaged 3.02 ± 0.29 Mg C ha^{-1} year^{-1} and 3.50 ± 0.38 Mg C ha^{-1} year^{-1} at Alp C (Table 3).

Wood respiration

Total estimated woody surface area of trees (>10 cm DBH) at Alp A was 20,000 m^2 ha^{-1} and 18,900 m^2 ha^{-1} for Alp C. Total estimated woody surface area of small trees (<10 cm DBH) was 433 m^2 ha^{-1} for Alp A and 480 m^2 ha^{-1} for Alp C. Based on this result, we calculated a stem area index (SAI) of 2.04 for Alp A and 1.94 for Alp C (Table 2). Woody respiration was not significantly different between the plots, with Alp A averaging 2.11 ± 0.06 µmol m^{-2} s^{-1} for all our measurements and Alp C averaging 2.11 ± 0.05 µmol m^{-2} s^{-1}.

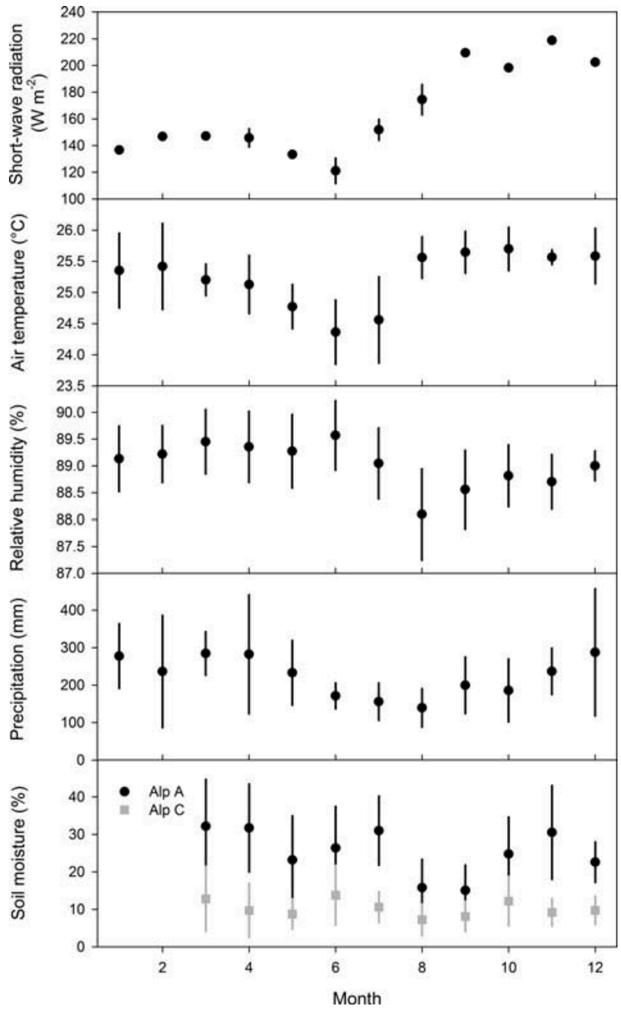

Figure 1. Climate data from a meteorological station located in a clearing 1 km from the plots at 3° 57′ 18.51″; S, 73° 25′10.69″ W for (a) total radiation (W m^{-2}), (b) average monthly temperature (°C), (c) atmospheric relative humidity (water vapour/saturated water vapour), and (d) average monthly precipitation (mm month^{-1}) and (e) soil moisture (%) in the Allpahuayo-Mishana National Reserve, near the city of Iquitos, Maynas Province, Department of Loreto, Peru. Error bars are standard deviations.

There was a significant positive linear relationship between woody NPP and trunk respiration for both Alp A and Alp C. We scaled these equations to the whole plot and found that the trees measured for woody respiration grew faster than average, and therefore we had to reduce our estimates for respiratory fluxes by 11% at Alp A and 5% at Alp C when scaled to the entire plot.

There was a significant seasonal cycle in wood respiration at both sites ($P < 0.001$), with respiration peaking during December for both sites and the minimum for both sites being in July (Figure 4). There was no significant difference between the sites when compared on a monthly timescale. Total annual woody respiration at Alp A was 9.63 ± 3.05 Mg C ha^{-1} year^{-1} and 8.11 ± 2.55 Mg C ha^{-1} year^{-1} for Alp C (Table 4).

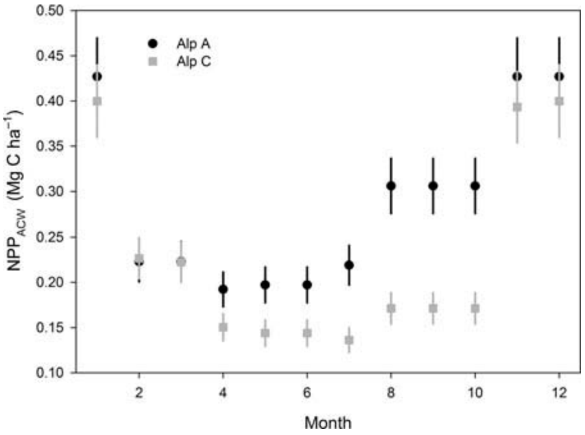

Figure 2. Above-ground woody NPP (Mg C ha^{-1} month^{-1}) measured by using dendrometer bands, every month over a 2-year period for two 1-ha plots: Alp A (black) and Alp C (grey), in the Allpahuayo-Mishana National Reserve, near the city of Iquitos, Maynas Province, Department of Loreto, Peru.

Leaf respiration and photosynthesis

There was significantly greater ($P < 0.05$) respiration in sun leaves at Alp C than Alp A but not in shade leaves (Table 4). The differences between sunlit and shaded respiration were not significant at either plot. Leaf photosynthetic capacity was significantly higher at Alp A than Alp C in both sunlit ($P < 0.01$) and shaded ($P < 0.05$) leaves (Table 4). Leaf area index (LAI) appeared aseasonal at both sites and averaged 5.6 ± 0.23 m^2 m^{-2} at Alp A, and 5.5 ± 0.24 m^2 m^{-2} at Alp C. Based on the leaf dark respiration measurements and measured LAI, we estimated annual canopy respiration to be 8.92 ± 3.00 Mg C ha^{-1} year^{-1} at Alp A and 11.35 ± 3.50 Mg C ha^{-1} year^{-1} at Alp C (Table 3).

Soil respiration

We calculated the average percentage respiration attributable to the rhizosphere by subtracting monthly values of tubes excluding rhizosphere respiration from those including rhizosphere and heterotrophic respiration. Averaged monthly values of rhizosphere respiration at Alp A were 25% of soil respiration, and this fraction did not show any seasonal variation (Figure 5). Averaged monthly values at Alp C were 31% of soil respiration. This did not vary much seasonally, with June to October values averaging 27%, and the rest of the year averaging 35%.

Total soil respiration did not have a strong seasonal cycle (Figure 4). Total annually averaged soil respiration was not significantly different between plots and averaged 18.12 ± 2.39 Mg C ha^{-1} year^{-1} at Alp A and 18.18 ± 1.71 Mg C ha^{-1} year^{-1} at Alp C. Total rhizosphere respiration was significantly different between plots ($P < 0.005$) and averaged 4.44 ± 0.92 Mg C ha^{-1} year^{-1} at Alp A and 6.38 ± 0.93 Mg C ha^{-1} year^{-1} at Alp C. Total heterotrophic soil respiration was not significantly different between plots and averaged 13.69 ± 2.64 Mg C ha^{-1} year^{-1}

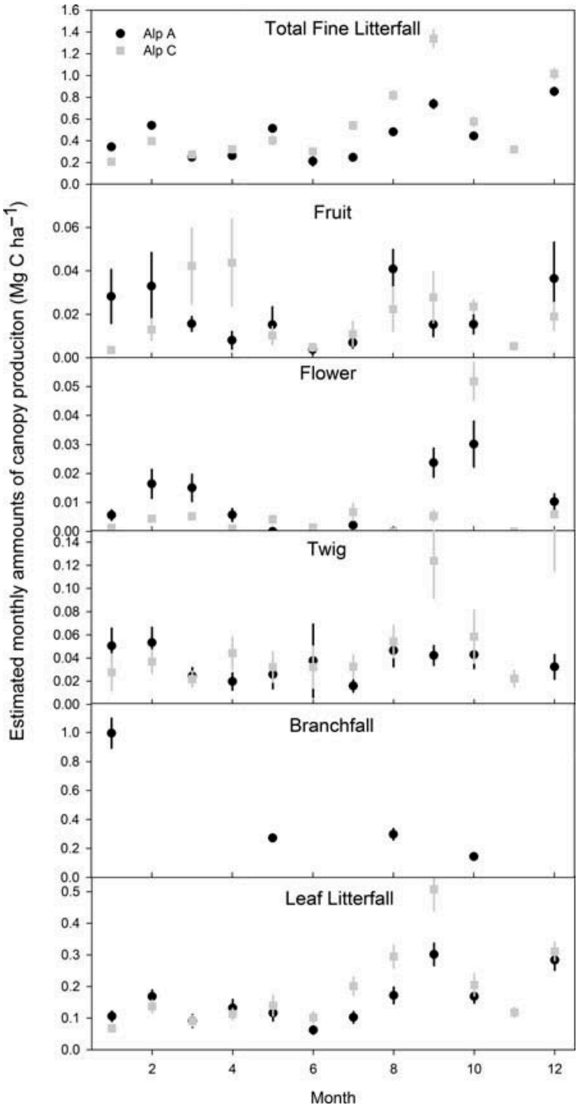

Figure 3. Sum of the monthly collections from 25 litter-traps of total litter, fruit, flowers, twig, branch, and leaf NPP (Mg C ha^{-1} month^{-1}) for two 1 ha plots Alp A (grey) and Alp C (black) in the Allpahuayo-Mishana National Reserve, near the city of Iquitos, Maynas Province, Department of Loreto, Peru. Error bars are standard errors.

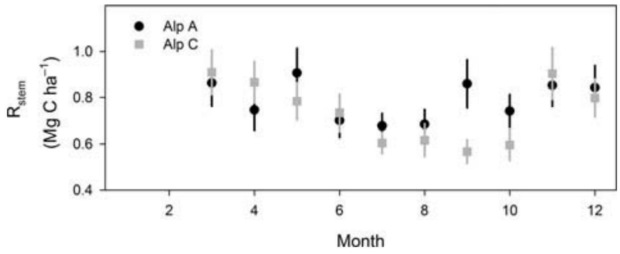

Figure 4. Above-ground wood respiration from collars on 25 trees measured every month multiplied by the total woody surface area of the plot (Mg C ha^{-1} month^{-1}) for two 1 ha forest plots Alp A (black circles) and Alp C (grey boxes) in the Allpahuayo-Mishana National Reserve, near the city of Iquitos, Maynas Province, Department of Loreto, Peru. Error bars are standard errors multiplied by woody surface area.

Table 4. Mean leaf dark respiration (R_{dark}) and light-saturated photosynthesis values (A_{sat}) for sun and shade leaves, Allpahuayo-Mishana National Reserve, near the city of Iquitos, Maynas Province, Department of Loreto, Peru, 2010.

	R_{dark} Sun	R_{dark} Shade	A_{sat} Sun	A_{sat} Shade
Alp A	0.56 ± 0.07**	0.67 ± 0.11	7.49 ± 0.50**	6.80 ± 0.72*
Alp C	0.89 ± 0.07	0.79 ± 0.05	4.88 ± 0.74	4.17 ± 0.72

Units are µmol m^{-2} s^{-1}. $^*P < 0.05$; $^{**}P < 0.01$.

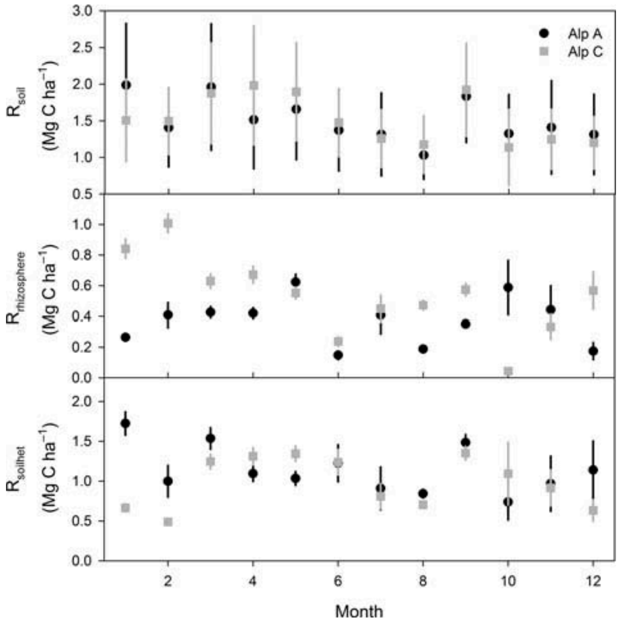

Figure 5. (top) Total soil respiration (R_{soil}) from 25 collars measured monthly (Mg C ha^{-1} month^{-1}), (middle) rhizosphere respiration (Mg C ha^{-1} month^{-1}) and (bottom) heterotrophic soil respiration (Mg C ha^{-1} month^{-1}) for a 2 year period for two 1 ha plots Alp A (black circles) and Alp C (grey boxes) in the Allpahuayo-Mishana National Reserve, near the city of Iquitos, Maynas Province, Department of Loreto, Peru. Autotrophic respiration was determined by an exclusion experiment ($N = 36$) where respiration was measured from tubes where roots and mycorrhizae were removed. Error bars are standard errors.

at Alp A and 11.80 ± 1.97 Mg C ha^{-1} year^{-1} at Alp C (Table 3).

NPP, GPP and CUE

We summed annually averaged fine root NPP, woody NPP, branch NPP, canopy NPP, and estimated coarse root NPP (as 20% of woody NPP) to estimate a plot level NPP of 14.14 ± 0.99 Mg C ha^{-1} year^{-1} for Alp A and 14.41 ± 0.94 Mg C ha^{-1} year^{-1} for Alp C (Figure 6). We summed annually averaged rhizosphere respiration, woody respiration, and canopy respiration to estimate total autotrophic respiration at 24.91 ± 4.48 Mg C ha^{-1} year^{-1} for Alp A and 27.46 ± 4.50 Mg C ha^{-1} year^{-1} for Alp C. We added total autotrophic respiration to total NPP to estimate total GPP at 39.05 ± 4.59 Mg C ha^{-1} year^{-1} for Alp A and 41.88 ± 4.60 Mg C ha^{-1} year^{-1} for Alp C. We divided total NPP

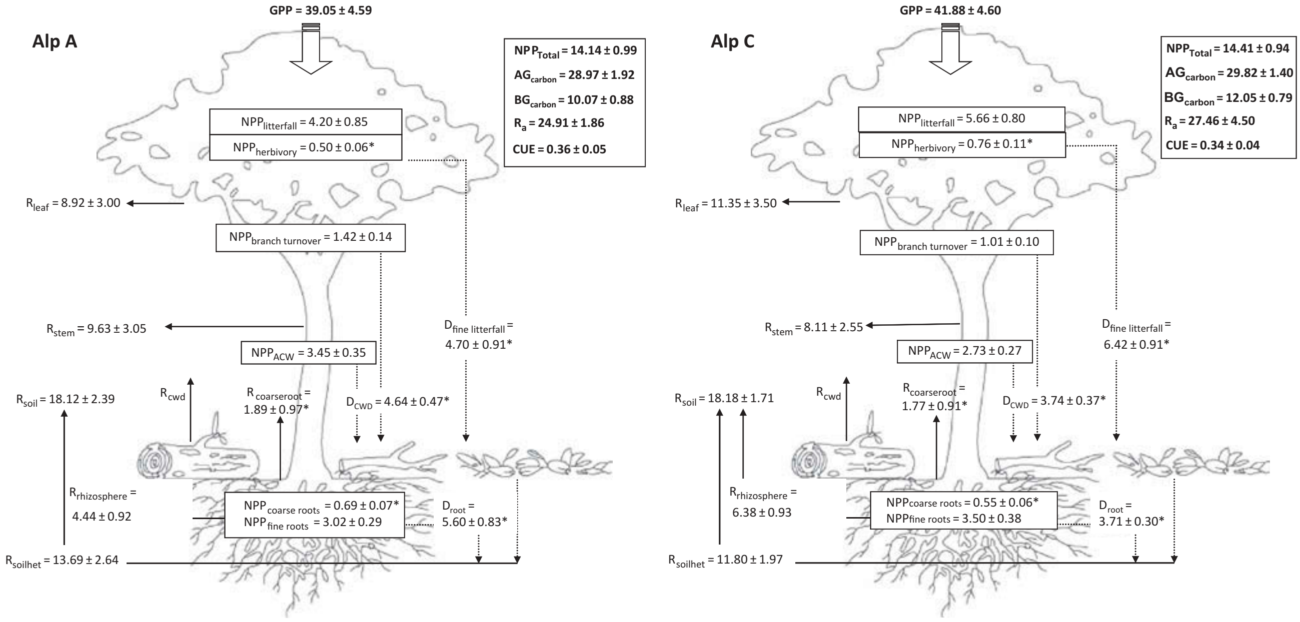

Figure 6. Diagram showing the magnitude and pattern of key carbon fluxes for two 1-ha forest plots Alp-A (left) and Alp-C (right) near the city of Iquitos, Maynas Province, Department of Loreto, Peru, within the Allpahuayo-Mishana National Reserve. Components with prefixes R, NPP and D denote respiration, net primary productivity and decomposition terms respectively. Detailed descriptions of C flux components measured are presented in Tables 1 and 2. All values are in units of Mg C ha^{-1} year^{-1}, with the exception of carbon use efficiency (CUE) which is calculated as total NPP/GPP. GPP, gross primary productivity; R_a, autotrophic respiration; R_h, heterotrophic respiration. Errors include sample error caused by spatial heterogeneity of the measured parameter within the study plots (standard error of the mean) together with an estimate of uncertainties due to measurement/equipment biases and up-scaling localised measurements to the plot level. The asterisk indicates an estimated (not measured) value.

by total GPP to estimate CUE at 0.36 ± 0.05 at Alp A and 0.34 ± 0.04 at Alp C (Table 3).

Discussion

The forests of north-eastern Peru are wetter than the mean value of Amazonian forests and completely lack a dry season (precipitation <100 mm month^{-1}) in most years. This is in contrast to a 4-month dry season reported in eastern Amazonian research sites, where much of the previous research on carbon cycling in tropical forests has taken place (Malhi et al. 2009). There are large edaphic differences between the plots, with Alp A being often waterlogged, but also having more biologically active phosphorus, while Alp C was on an unstable substrate where tree falls may have been more prevalent, with less biologically active phosphorous. However, both plots had relatively high nutrient concentrations compared with the eastern Amazon (Quesada et al. 2010).

Perhaps the most interesting initial difference between the two plots was the large difference in overall biomass (Alp A had 150.60 Mg C ha^{-1} and Alp C had 96.28 Mg C ha^{-1}), which was not caused by differences in productivity since both sites had similar total GPP values. Instead, it was driven mainly by lower stem density at the sandy site (476 stems ha^{-1}) versus 576 stems ha^{-1}, which was possibly a function of being based on sand which is generally less stable than clay. Both plots were surprising dynamic, amongst the most dynamic in Amazonia, with stem biomass residence times of 41 (Alp A) and 33 years (Alp C). The high dynamism at Alp C may be a function of the poor structural support for the trees of the white sand substrate, and previous studies have found more treefall (Phillips et al. 2004; Chao et al. 2008).

Does the lower biomass in Alp C lead to greater allocation of NPP and GPP towards wood growth? Our data indicate that this was not the case; instead, the lower stem density site (Alp C) invested more NPP into canopy growth (45% vs. ca. 33% at Alp A), thus increasing photosynthetic potential.

Although total GPP at both sites was similar, leaf maximum photosynthetic capacity was significantly greater at Alp A than Alp C (Table 4). This may be associated with the higher biologically active soil phosphorus concentrations at Alp A versus Alp C (Table 5) (Quesada et al. 2011). Phosphorus is generally considered the limiting nutrient in tropical forests (Vitousek 1984; Quesada et al. 2010) and may have a strong impact on leaf level photosynthesis. Average leaf maximum photosynthetic capacity at Alp A was 14% higher than Alp C. However, leaf production was 38% greater at Alp C than Alp A, therefore lower photosynthetic capacity may have partially been offset by more, newer leaves which tend to have higher photosynthetic rates than older leaves (Doughty and Goulden 2008), resulting in similar total GPP values for the two sites.

One might have expected less allocation to roots in the more fertile clay soil but no significant difference was observed between plots. Allocation to roots was 21 ± 3%

Table 5. Leaf P and N data derived from (Fyllas et al. 2009) and soil chemistry data averaged from 0–30 cm soil depth from Quesada et al. (2010).

Plot	Alp A gleysol ALP-11	Alp A alisols ALP-12	Alp C sandy ALP-30
Leaf P (mg g^{-1})	0.84	0.78	1.02
Leaf N (mg g^{-1})	17.60	20.32	20.28
pH	4.47	4.26	4.07
Total N (%)	0.13	0.06	0.08
Total C (%)	1.71	0.68	1.13
C:N	12.70	11.07	13.47
P_a (mg kg^{-1})	19.72	23.76	24.77
P_{ex} (mg kg^{-1})	52.80	75.57	36.57
P_{Total} (mg kg^{-1})	140.91	110.30	37.64
Σ_{RB}	114.65	40.60	4.07
Ca_{ex} (mmol$_c$ kg^{-1})	0.45	1.46	2.57
Mg_{ex}	0.34	1.28	0.98
K_{ex}	0.45	1.12	0.65
Na_{ex}	0.09	0.15	0.05
Al_{ex}	23.28	32.23	0.62
Σ_B	1.33	4.01	4.24
Sand (%)	0.78	0.53	0.82
Clay (%)	0.10	0.21	0.02
Silt (%)	0.13	0.27	0.16

N, total soil nitrogen; C, total soil carbon; P_{ex}, extractable pool (total residual, or biologically active P); P_a, readily available pool; P_{Total}, total soil phosphorus pool (mg kg^{-1}); Σ_{RB}, total reserve bases; Ca_{ex}, Mg_{ex}, K_{ex}, Al_{ex}, exchangeable calcium, magnesium, potassium and aluminum concentrations; Σ_B, sum of exchangeable bases; I_E, effective soil cation exchange capacity (mmol$_c$ kg^{-1}). Total nitrogen and carbon are given in %. For detailed methods and descriptions see Quesada et al. (2010).

at Alp A and 24 ± 3% at Alp C (Table 6). These allocation patterns compare with a mean allocation of 27 ± 11% towards fine roots in a recent review of allocation patterns in tropical forests (Malhi et al. 2011). The plots may have shown similar root growth because readily available phosphorus, which is essentially identical between the plots, may be more important for root growth than the total pool of soil P, which is larger in Alp A.

It has been suggested that there would be greater allocation of GPP to below ground at warmer sites because, since temperature will not constrain growth as it would in colder regions, growth will instead be constrained by limitations of nutrients and water (Litton and Giardina 2008). Since our sites are among the warmest on the planet, we might expect the highest allocation below ground. Total below-ground carbon flux can be between 21–75% of GPP (Litton et al. 2007), and our estimates (29% and 26%) are towards the lower end of that range, which diverge from the predictions of the theory. However, the lack of a dry season at our sites will also reduce the need for an extensive root system to supply water, which may also explain this result.

Some of our measurements showed a surprising seasonality given the complete lack of seasonality in water stress, which is generally thought to drive seasonal patterns in tropical forests. There was significant seasonality in woody NPP, with peaks in growth corresponding to peaks in increased solar radiation. There was also an increase in litterfall during periods of increased solar radiation. Between January and June there was less than 150 W m^{-2} irradiance, and this increased to almost 200 W m^{-2} between July to December. This peak in litterfall often corresponds to a peak in leaf flush (Doughty and Goulden 2008).

Table 6. Patterns of mean (±SE) above/below-ground allocation, allocation of NPP, GPP and autotrophic respiration in two 1-ha plots Alp A and Alp C with standard errors (SE) Allpahuayo-Mishana National Reserve, near the city of Iquitos, Maynas Province, Department of Loreto, Peru.

Total carbon allocation	Alp A (± SE)	Alp C (± SE)
AG carbon (Mg C ha^{-1} year^{-1})	28.97 (±4.50)	29.83 (±4.49)
BG carbon (Mg C ha^{-1} year^{-1})	10.07 (±0.99)	12.05 (±1.02)
AG fraction (%)	0.74 (±0.07)	0.71 (±0.06)
BG fraction (%)	0.26 (±0.03)	0.29 (±0.03)
Allocation of NPP		
Canopy (%)	0.33 (±0.10)	0.45 (±0.09)
Wood (%)	0.45 (±0.10)	0.31 (±0.07)
Fine roots (%)	0.21 (±0.03)	0.24 (±0.03)
Allocation of GPP		
Canopy (%)	0.35 (±0.11)	0.42 (±0.09)
Wood (%)	0.46 (±0.09)	0.34 (±0.07)
Rhizosphere (%)	0.19 (±4.50)	0.24 (±0.03)
Partitioning of autotrophic respiration		
Canopy (%)	0.36 (±0.06)	0.41 (±0.03)
Wood (%)	0.46 (±0.06)	0.35 (±0.04)
Rhizosphere (%)	0.18 (±0.04)	0.23 (±0.03)

These forests have very high total estimated GPP, amongst the highest noted in Amazonia. These high productivities are arrived at despite neither soil type being optimal for growth, one being occasionally waterlogged and the other being a structurally poor sandy soil. It appears that the very warm, wet, conditions overcome these constraints to productivity. It should be noted that this particular white sand site appears especially productive, and is probably not representative of white sand forests across the Amazon Basin. For example Arãgao et al. (2009) reported the NPP of a forest growing on white sands at Zafire, Colombia, to be 9.3 ± 1.26 Mg C ha^{-1}, compared with 14.41 ± 0.94 Mg C ha^{-1} for Alp C.

Conclusions

Overall, the lack of a dry season and relatively high photosynthetic capacity of the leaves seems to have contributed to the very high values of GPP (39.05 and 41.88 Mg C ha^{-1} year^{-1}), higher than those reported for forests in Brazilian Amazonia on Ferralsols (Malhi et al. 2009). CUE was also higher, which may be related to the high forest dynamism and natural disturbance rate. These two factors combine to result in amongst the highest NPP and GPP values reported for Amazonia.

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