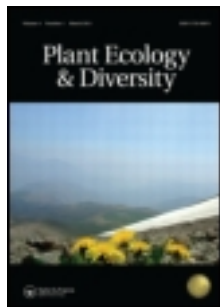


This article was downloaded by: [Purdue University]

On: 14 September 2013, At: 20:23

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Plant Ecology & Diversity

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tped20>

The production, allocation and cycling of carbon in a forest on fertile terra preta soil in eastern Amazonia compared with a forest on adjacent infertile soil

Christopher E. Doughty^a, Daniel B. Metcalfe^b, Mauricio C. da Costa^c, Alex A.R. de Oliveira^c, G. F.C. Neto^c, João A. Silva^c, Luiz E.O.C. Aragão^d, Samuel S. Almeida^e, Carlos A. Quesada^f, Cecile A.J. Girardin^a, Kate Halladay^a, Anthony C.L. da Costa^c & Yadvinder Malhi^a

^a Environmental Change Institute, University of Oxford, Oxford, UK

^b Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

^c Universidade Federal do Pará Centro de Geociências, Belém, Brasil

^d College of Life and Environmental Sciences, University of Exeter, Exeter, UK

^e Museu Paraense Emilio Goeldi, Belém, Brasil

^f Instituto Nacional de Pesquisas da Amazônia, Manaus, Brasil

Published online: 30 Jul 2013.

To cite this article: Christopher E. Doughty, Daniel B. Metcalfe, Mauricio C. da Costa, Alex A.R. de Oliveira, G. F.C. Neto, João A. Silva, Luiz E.O.C. Aragão, Samuel S. Almeida, Carlos A. Quesada, Cecile A.J. Girardin, Kate Halladay, Anthony C.L. da Costa & Yadvinder Malhi, *Plant Ecology & Diversity* (2013): The production, allocation and cycling of carbon in a forest on fertile terra preta soil in eastern Amazonia compared with a forest on adjacent infertile soil, *Plant Ecology & Diversity*, DOI: 10.1080/17550874.2013.798367

To link to this article: <http://dx.doi.org/10.1080/17550874.2013.798367>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

The production, allocation and cycling of carbon in a forest on fertile *terra preta* soil in eastern Amazonia compared with a forest on adjacent infertile soil

Christopher E. Doughty^{a*}, Daniel B. Metcalfe^b, Mauricio C. da Costa^c, Alex A.R. de Oliveira^c, G.F.C. Neto^c, João A. Silva^c, Luiz E.O.C. Aragão^d, Samuel S. Almeida^{e†}, Carlos A. Quesada^f, Cecile A.J. Girardin^a, Kate Halladay^a, Anthony C.L. da Costa^c and Yadvinder Malhi^{a*}

^aEnvironmental Change Institute, University of Oxford, Oxford, UK; ^bDepartment of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden; ^cUniversidade Federal do Pará Centro de Geociências, Belém, Brasil; ^dCollege of Life and Environmental Sciences, University of Exeter, Exeter, UK; ^eMuseu Paraense Emilio Goeldi, Belém, Brasil; ^fInstituto Nacional de Pesquisas da Amazônia, Manaus, Brasil

(Received 16 March 2012; final version received 17 April 2013)

Background: *Terra preta do índio* or 'dark earth' soils formed as a result of a long-term addition of organic matter by indigenous peoples in Amazonia.

Aims: Here we report on the first study of productivity, allocation and carbon cycling from a *terra preta* plot in eastern Amazonia (Caxiuanã, Pará, Brazil), and contrast its dynamics with a nearby plot on infertile soil (ferralsols).

Methods: We determined total net primary production (NPP) for fine roots, wood, and canopy and total autotrophic respiration (rhizosphere, wood, and canopy respiration) from two 1-ha plots on contrasting soils.

Results: Both gross primary productivity (GPP) (35.68 ± 3.65 vs. 32.08 ± 3.46 Mg C ha⁻¹ year⁻¹) and carbon use efficiency (CUE) (0.44 ± 0.06 vs. 0.42 ± 0.05) were slightly higher at the *terra preta* plot. Total NPP (15.77 ± 1.13 Mg C ha⁻¹ year⁻¹ vs. 13.57 ± 0.60 Mg C ha⁻¹ year⁻¹) and rates of fine root production (6.41 ± 1.08 vs. 3.68 ± 0.52 Mg C ha⁻¹ year⁻¹) were also greater at the *terra preta* plot vs. the tower plot.

Conclusions: Forests on *terra preta* soil fix slightly more carbon and allocate slightly more of that carbon towards growth than forests on the infertile plot, which leads to greater total NPP, which was disproportionately allocated to fine roots. However, since increased fine root NPP was partially offset by increased heterotrophic soil respiration, the increased root growth was unlikely to greatly enhance soil carbon stocks in *terra preta* soils.

Keywords: anthrosol; carbon use efficiency (CUE); gross primary productivity (GPP); net primary production (NPP); *terra preta*; tropical forests

Introduction

As the largest existing contiguous patch of old-growth rain forest existing in the world today, the Amazon forest remains, for many, the archetype of a pristine wilderness. Initially, the Amazon lowland basin was seen as too infertile to support large human populations. To survive in the forest, it was assumed that farming would soon exhaust soil nutrients, thereby necessitating regular clearing of new land in a form of low-intensity, shifting agriculture incapable of supporting high population densities (Meggers 1971). However, evidence is amassing for the existence of substantial pre-Columbian population centres (Roosevelt 1993). Of particular interest for scientists and policy makers is the presence of fertile dark earth (*terra preta do índio*) soil patches that seem to have been formed around long-term indigenous settlements (Denevan 2001).

The original *terra preta* soils are thought to have been created by pre-Colombian Amazonians through low-heat, smouldering, domestic fires that were used for cooking and heating (Smith 1980; Smith et al. 1999). Radiocarbon ages of *terra preta* soils in Santarém, in the Amazonian state of

Pará, give a date of 1775 ± 325 years BP based on charcoal pieces found at ~60-cm soil depth (Glaser et al. 1999).

Terra preta soils may have been a mechanism of increasing productivity on the more common nutrient-poor ferralsol that predominates in the eastern Amazon region. The extent of the *terra preta* soil type in the Amazon Basin is an interesting and yet unresolved question although an average area of ca. 20 ha is typical (Smith 1980), but areas up to 350 ha have also been reported (Smith et al. 1999). A recent study found that the *terra preta* soil type is common in the eastern Amazon but much less common elsewhere in western and central Amazonia (McMichael et al. 2012). Many *terra preta* plots were abandoned and covered in forests following the population declines of indigenous populations, although many are still farmed because of their high fertility.

Soil fertility plays a central role in the carbon cycling dynamics of the Amazon forest. There is a gradient in increasing soil fertility from the north-east to the south-west (Quesada et al. 2010), which has been shown to affect biomass and carbon cycling (Malhi et al. 2004,

*Corresponding authors. Email: chris.doughty@ouce.ox.ac.uk; yadvinder.malhi@ouce.ox.ac.uk

†Deceased

2006). However, other confounding biogeographical variables could affect these results and an ideal experiment would be to place a high soil fertility zone (such as *terra preta*) in the low-fertility eastern Amazon.

Interest in the *terra preta* soil type has increased because biochar, which has similar properties to *terra preta*, has recently received attention due to its potential mitigating role against climate change (Woolf et al. 2010). Yet, despite interest in *terra preta* and biochar, there is currently almost no information about the carbon cycling of the forests growing on the *terra preta* soil type. There are two main reasons that understanding the properties of these soils on ecosystem ecology is important. Firstly, it can help differentiate between the role of soil fertility and climate on productivity, although different land-use histories may also complicate this. Secondly, there is widespread interest in using biochar in agricultural zones worldwide as a climate change mitigation tool, but there is little information about the long-term impacts of biochar on the productivity and allocation of carbon.

Recent studies have detailed changes in total net primary production (NPP) along an elevation transect (Girardin et al. 2010) and across the Amazon basin (Aragao et al. 2009). However, this data is difficult to relate to gross primary production (GPP) and other ecosystem properties if complete autotrophic respiration measurements are not made. In this paper, we compare the cycling and allocation of carbon in a 1-ha plot where the soil is predominantly *terra preta* and compare this to a 1-ha plot dominated by ferralsol soil, typical to the eastern Amazon. We present results for seasonality, NPP, GPP, and carbon use efficiency (CUE) averaged over a two-year period. We asked the following specific questions:

- (1) Does a forest growing on the *terra preta* soil type have higher growth rates and stand-level productivity (GPP and NPP) compared to the more nutrient-poor ferralsol soil type?
- (2) Do patterns of CUE and the allocation of NPP differ between the two plots?
- (3) Are there differences in the seasonal patterns of carbon cycling between the two plots?

Materials and methods

Plot characteristics

The *terra preta* plot (plot code CAX-08 in the RAINFOR Amazon forest inventory network) was a late successional secondary forest with a large proportion of fruit trees, on an isolated patch (<2 ha) of fertile dark earth or *terra preta do indio*. The original soil on the tower plot (termed 'tower' because of the presence of a flux tower; RAINFOR code CAX-06) became progressively enriched by the activities of local inhabitants between the years 1280 to 1600 AD (Lehmann et al. 2003). The *terra preta* plot was chosen as one of the few areas with *terra preta* soil inside the Caxiuanã National Forest Reserve (1° 43' S, 51° 27' W)

and whose vegetation had remained largely undisturbed for at least 40 years. The *terra preta* plot was located about 15 km to the south of the tower plot, by the edge of a large inland river bay, the Baía de Caxiuanã. The species composition of the *terra preta* plot was that of an old, abandoned agroforestry system, with Brazil nut (*Bertholletia excelsa*), kapok (*Ceiba pentandra*), and also paleotropical tree crops including coffee (*Coffea*) and orange (*Citrus*). Given their high fertility, it was almost impossible to find an accessible patch of *terra preta* that has not been used for agroforestry or farming in recent times. The selected plot was abandoned in the 1950s following the creation of the Caxiuanã National Forest Reserve, and so has undergone some extent of re-colonisation by native forest species, while still being far from a mature forest. The water-side location of the *terra preta* plot results in a substantially different microclimate from that of the inland tower plot, with high solar radiation (the large cool water area of the bay suppresses cloud formation close to the bay) and higher temperatures. The tower plot was a tall primary forest (35 m canopy height) situated on a clay-rich geric alumnice ferralsol (alumnice, hyperdistric, clayic) (Quesada et al. 2010, 2011), near an eddy covariance flux tower.

Carbon fluxes

The protocols used to estimate ecosystem C flux components within the 1-ha plot (divided into 25 20 × 20 m² subplots) were largely based on those developed by the RAINFOR-GEM network. Measurements were distributed evenly throughout 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:

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

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

This neglects several small NPP terms, such as NPP lost as volatile organic emissions or litter decomposed in the canopy. Total R_a (autotrophic respiration) is estimated as

$$R_a = R_{\text{leaves}} + R_{\text{stems}} + R_{\text{rhizosphere}} \quad (3)$$

Here we count root exudates and transfer to mycorrhizae as a portion of $R_{\text{rhizosphere}}$ rather than NPP . In quasi-steady-state conditions (and on annual timescales or longer where there no net change in plant non-structural carbohydrate

Table 1. Methods for intensive studying of carbon dynamics for the tower and *terra preta* plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil (see also online supplemental material and RAINFOR-GEM manual 2012).

Component	Data collection details	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 (Chave et al. 2005). One 20×20 m ² subplots were established to carry out censuses on small trees (2.5–10 cm DBH) using calipers, and data was scaled up to one hectare. Seasonal growth: dendrometers were installed on all trees > 10 cm DBH in each plot to determine the spatial-temporal and seasonal variation in growth.	2004–2007	Every year (trees ≥ 10 cm DBH) Every 6 months (trees 2.5–10 cm DBH)
Branch turnover net primary productivity ($NPP_{branch\ turnover}$)	Branches (excluding those fallen from dead trees) were surveyed within four 1×100 m ² transects; small branches were cut to include only the transect-crossing component, removed, and weighed. Larger branches had their dimensions taken (diameter at three points) and all were assigned a wood density value according to their decomposition class.	2005–2011	Every 3 months
Litterfall net primary productivity ($NPP_{litterfall}$)	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.	March 2010–December 2011	Every 2 months
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. LAI was estimated from these images using CAN-EYE software (Demarez et al. 2008).	January 2009–December 2011	Every 14 days
Loss to leaf herbivory ($NPP_{herbivory}$)	Leaves collected in the 25 litterfall traps in each plot were photographed prior to being dried. Leaf area was determined with image analysis software (ImageJ, NIH, USA) to calculate the area of each individual leaf including the damage incurred by herbivory.	July 2009–March 2011	Every 2 months
Coarse root net primary productivity ($NPP_{coarse\ roots}$)	This component of productivity was not measured directly and was estimated by assuming that coarse root productivity was 0.21 ± 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).	January 2009–December 2011	Every month
Fine root net primary productivity ($NPP_{fine\ roots}$)	Sixteen in-growth 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 min. Root-free soil was then re-inserted into the ingrowth core. Collected roots were thoroughly rinsed, oven-dried at 80 °C, and weighed.	n/a	Not directly measured
Below-ground net primary productivity (NPP_{BG})		July 2009–February 2011	Every 3 months

(Continued)

Table 1. (Continued)

	Component	Data collection details	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 PP Systems Amesbury, MA, USA) and soil respiration chamber (SRC-1) sealed to a permanent collar in the soil.	July 2009–April 2011	Every month
	Soil CO ₂ efflux partitioned into autotrophic ($R_{\text{rhizosphere}}$) and heterotrophic (R_{soilhet}) components	At four points at each corner of the plot, we placed plastic tubes of 12 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 windows with fine mesh to exclude fine roots but not mycorrhizae. 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.	July 2009–April 2011	Every month
	Canopy respiration (R_{canves})	In each plot, leaf dark respiration was recorded for 30 trees with an IRGA and specialised 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).	January–February 2007	Measured over 2 months
	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 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.	July 2009–December 2010	Every 2 months
	Coarse root respiration ($R_{\text{coarse roots}}$)	This component of respiration was not measured directly and was estimated by multiplying estimated above-ground live wood respiration by 0.21 (same ratio used in this study to estimate coarse root biomass and growth – see above).	n/a	Not directly measured

Table 2. Data analysis techniques for intensive studying of carbon dynamics for the tower and *terra preta* plots in the Caxiuana National Forest Reserve, eastern Amazonia, Brazil (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 47.4% carbon (Martin and Thomas 2011).
	Branch turnover net primary productivity ($NPP_{branch\ turnover}$)	See RAINFOR-GEM manual (Version 2.2, 2012, p. 61) for description.
	Litterfall net primary productivity ($NPP_{litterfall}$)	$NPP_{litterfall}$ is calculated as follows: $NPP_{litterfall} = NPP_{canopy} - \text{loss to leaf herbivory}$. Litterfall is separated into different components, oven-dried at 80 °C to constant mass and weighed. Litter is estimated to be 48.2% carbon, based on mean Amazonian values (S. Patiño, unpublished analysis).
	Leaf area index (LAI)	LAI estimated using ‘true LAI’ output from the Can-eye program which account for clumping of foliage, and assuming a fixed leaf inclination angle of 42.7°, based on average estimates at the tower plot using the CAN-EYE program (Demarez et al. 2008). Leaves were separated into sunlit and shaded fractions using the following equation: $F_{sunlit} = (1 - \exp(-K * LAI)) / K$ 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°.
	Loss to leaf herbivory ($NPP_{herbivory}$)	The fractional herbivory (H) for each leaf was then calculated as: $H = (A_h - A_{nh}) / A_{nh}$ 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 ($NPP_{coarse\ roots}$)	See RAINFOR-GEM manual (Version 2.2, 2012, p. 47) for description and range of root:shoot ratio.
	Fine root net primary productivity ($NPP_{fine\ roots}$)	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 (Metcalf et al. 2007) and used to predict root extraction beyond 40 min (up to 100 min); we estimate that there was an additional ~25% correction factor for fine roots not collected within 40 min. Correction for fine root productivity below 30 cm depth (Galbraith et al., in review) 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 ($R_{rhizosphere}$) and heterotrophic ($R_{soilnet}$) 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 shaded and sunlit leaves were multiplied by the respective estimated fractions of total LAI. The wet season respiration mean was applied to all months with > 100 mm rain; the dry season months, measured dry season respiration was linearly scaled by the soil moisture saturation to allow for more continuous variation of leaf respiration. 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 bole surface area (SA) for each tree, estimated with the following equation (Chambers et al. 2004): $\log(SA) = -0.015 - 0.686 \log(DBH) + 2.208 \log(DBH)^2 - 0.627 \log(DBH)^3$ where H is tree height, and DBH 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 ($R_{coarse\ roots}$)	In recognition of the substantial uncertainty in this estimate, we assigned a 50% error (± 0.10) to the multiplying factor.	

storage), *GPP* should be approximately equal to the sum of *NPP* and R_a . Hence, we estimated *GPP* as

$$GPP = NPP_{AG} + NPP_{BG} + R_a \quad (4)$$

We estimated the *CUE* as *NPP* divided by *GPP*:

$$CUE = \frac{(NPP_{AG} + NPP_{BG})}{(NPP_{AG} + NPP_{BG} + R_a)} \quad (5)$$

Meteorological data

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

Statistics and error analysis

A key consideration is assignment and propagation of uncertainty in our measurements. There are two primary types of uncertainty. Firstly, there is 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 is a systematic uncertainty associated with either unknown biases in measurement or uncertainties in scaling measurements to the plot level. Examples of unknown biases include the possibility of soil CO_2 in the transpiration stream affecting the stem and CO_2 efflux measurements, and uncertainties in scaling include 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 assume that most *NPP* terms are measured fairly precisely and sampled without large biases: hence, the *NPP* component measurements are dominated by sampling uncertainty, which can be reliably estimated assuming a normal distribution. On the other hand, some of the main autotrophic respiration terms are dominated by systematic uncertainty. This systematic uncertainty can be very hard to reliably quantify; here, in each case we make an explicit and conservative estimate of the systematic uncertainty of key variables. Our assumptions about the uncertainty in each measurement are clearly described (Table 2) and presented in the results table (Table 4).

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 region of the Caxiuaná National Forest Reserve containing our plots had moderate seasonality in rainfall, ranging from over 200 $mm\ month^{-1}$ in the peak rainy season (January to April) to less than 100 $mm\ month^{-1}$ for four to five months of the year (August to November) (Figure 1). There was a strong seasonality in solar radiation, with greater solar radiation corresponding to periods with reduced rainfall. There was a slight seasonality in air temperature, with warmer temperatures corresponding to the dry season. The 6-year mean annual rainfall was ca. 2556 $mm\ year^{-1}$ at the tower plot and 2311 $mm\ year^{-1}$ at the *terra preta* plot; and the long-term mean annual air temperature was ca. 25.8 °C at the tower plot and 27.2 °C at the *terra preta* plot (see online supplemental material, Table S1). Soil moisture content (top 18 cm) was similar in the tower plot ($27.1 \pm 0.27\%$) to the *terra preta* plot

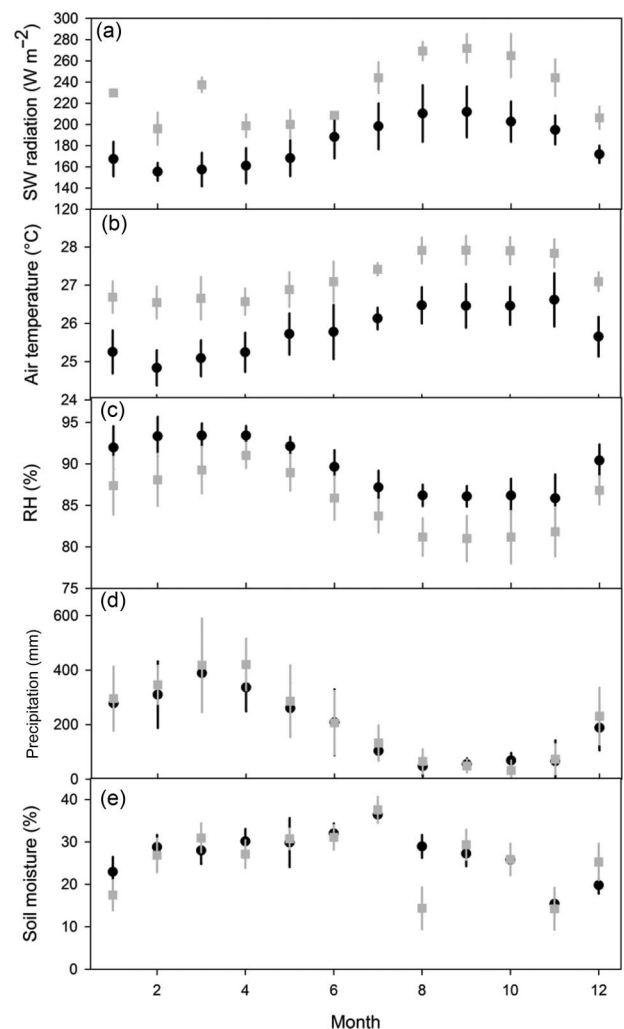


Figure 1. Climate data from a meteorological station for (a) total radiation ($W\ m^{-2}$); (b) average monthly temperature ($^{\circ}C$); (c) atmospheric relative humidity (RH, water vapour/saturated water vapour); (d) average monthly precipitation ($mm\ month^{-1}$); and (e) soil moisture (%) for the tower (black circles) and *terra preta* (grey squares) plots in the Caxiuaná National Forest Reserve, eastern Amazonia, Brazil. Error bars are standard deviations.

($26.6 \pm 0.31\%$ water), varying from a maximum in July to a minimum in November.

Fine root NPP

The tower plot had less total fine-root NPP than in the *terra preta* plot, averaging 3.68 ± 0.52 Mg C ha⁻¹ year⁻¹ in the tower plot and 6.41 ± 1.08 Mg C ha⁻¹ year⁻¹ in the *terra preta* plot (Table 4). Fine-root NPP showed much seasonality in both plots and increased by 52% in February compared to August in the tower plot and by 48% in the *terra preta* plot (Figure 2).

Woody NPP

Average (\pm SE) wood density in the tower plot was significantly greater ($P < 0.001$) at 0.68 ± 0.005 g cm⁻³ compared with 0.57 ± 0.006 g cm⁻³ in the *terra preta* plot (Table 3). We estimated a mean small tree (>10 and <20 cm diameter at breast height (DBH)) height of 12.8 ± 1.2 m for the tower plot and 12.8 ± 1.3 m for the *terra preta* plot, mean medium tree (>20 and <40 cm DBH) height of

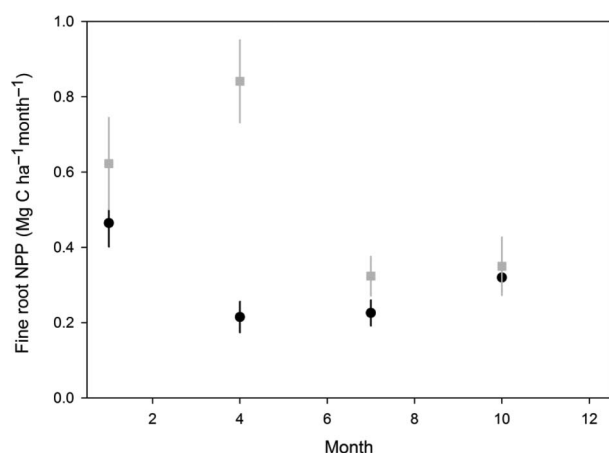


Figure 2. Fine root NPP (Mg C ha⁻¹ month⁻¹) from 16 ingrowth cores collected every three months over a two-year period for the tower (black circles) and *terra preta* plots (grey squares) in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Error bars are standard errors.

18.2 ± 1.8 m for the tower plot and 17.2 ± 1.5 m for the *terra preta* plot, and mean tall tree (>40 cm DBH) height of 25.3 ± 3.2 m for the tower plot and 27.2 ± 5.5 m for the *terra preta* plot. Stem density (>10 cm) was 448 stems ha⁻¹ at the tower plot and 547 stems ha⁻¹ at the *terra preta* plot. We estimated an initial above-ground biomass (>10 cm DBH) of 173.4 Mg C ha⁻¹ for the tower plot and 102.8 Mg C ha⁻¹ for the *terra preta* plot. The tower plot had an average small tree biomass of 6.1 Mg C ha⁻¹ and 8.1 Mg C ha⁻¹ at the *terra preta* plot. Adding the large tree and small tree biomass, we estimate a total biomass of 179.4 Mg C ha⁻¹ at the tower plot, and 110.9 Mg C ha⁻¹ at the *terra preta* site.

We measured the DBH of all stems >10 cm in 2004, 2005, 2006, and 2007 to calculate above-ground woody NPP. The tower plot averaged 2.60 Mg C ha⁻¹ year⁻¹ and the *terra preta* averaged 2.50 Mg C ha⁻¹ year⁻¹. Average small tree above-ground woody growth was 0.42 Mg C ha⁻¹ year⁻¹ at the tower plot and 0.50 Mg C ha⁻¹ year⁻¹ at the *terra preta* plot. Adding the large tree and small tree woody NPP, we estimated total above-ground woody NPP to be 3.02 Mg C ha⁻¹ year⁻¹ at the tower plot, and 3.00 Mg C ha⁻¹ year⁻¹ at the *terra preta* plot (Table 4).

To estimate the effect of moisture expansion during the wet season on tree growth, we separated the trees with almost no annual tree growth (woody NPP < 0.1 kg C tree⁻¹, $n = 46$ for the tower plot, $n = 64$ for the *terra preta* plot) and measured their seasonal woody NPP trends. On these slow-growing trees we found an average seasonal amplitude that peaked in July and was lowest in November. We attributed the expansion of the dendrometer bands between these periods to the seasonal effect of moisture expansion and estimated it at 0.036 Mg C ha⁻¹ year⁻¹ on the tower plot and 0.03 Mg C ha⁻¹ year⁻¹ on the *terra preta* plot. Even after correcting for moisture expansion, there was a strong seasonality to woody NPP in the tower plot with a peak in woody growth in January and a minimum in October (Figure 3). *Terra preta* showed a similar, but more extreme, seasonal pattern with a peak in December and a minimum in August (Figure 3). We estimated coarse root NPP as 21% of stem NPP and therefore 0.55 Mg C ha⁻¹ year⁻¹ for the tower plot and 0.53 Mg C ha⁻¹ year⁻¹ for the *terra preta* plot.

Table 3. Average forest LAI, wood density, tree height, stem density, SAI, and biomass for large (>10 cm) and small (<10 cm) trees between the tower and *terra preta* plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil, and the percentage differences between the two.

Variable	Tower	<i>Terra preta</i>	Difference (%)
Leaf area index (LAI) (m ² m ⁻²)	5.0 ± 0.19	5.3 ± 0.21	6
Wood density (g cm ⁻³)	0.68	0.57	-19
Mean tree height (m)	18.4 ± 0.25	16.7 ± 0.16	-10
Stem density (stems ha ⁻¹)	448	547	18
Stem area index (SAI) (m ² wood m ⁻² ground)	1.65	1.63	-1
Biomass >10 cm (Mg C ha ⁻¹)	173.4	102.8	-69
Biomass <10 cm (Mg C ha ⁻¹)	6.1	8.1	25

Table 4. Total yearly averaged litterfall NPP, components of litterfall NPP, herbivory, branch NPP, above-ground coarse wood NPP, coarse root NPP, fine root NPP, canopy dark respiration, wood respiration, rhizosphere respiration, coarse root respiration, soil heterotrophic respiration, total autotrophic respiration, NPP, GPP and CUE for the tower and *terra preta* plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil.

	Tower			<i>Terra preta</i>		
	Mean	Sample error	Total error	Mean	Sample error	Total error
$NPP_{\text{finelitter}}$	5.03	0.07	0.07	4.52	0.18	0.18
NPP_{leaf}	3.68	0.05	0.05	2.90	0.15	0.15
NPP_{flower}	0.18	0.02	0.02	0.18	0.04	0.04
NPP_{fruit}	0.24	0.02	0.02	1.12	0.03	0.03
NPP_{twigs}	0.80	0.03	0.03	0.45	0.05	0.05
$NPP_{\text{herbivory}}$	0.24	0.00	0.00	0.21	0.01	0.01
$NPP_{\text{branch turnover}}$	1.06	0.12	0.12	1.10	0.11	0.11
$NPP_{ACW > 10\text{cm dbh}}$	2.60	0.26	0.26	2.50	0.25	0.25
$NPP_{ACW < 10\text{cm dbh}}$	0.42	0.04	0.04	0.42	0.04	0.04
$NPP_{\text{coarseroot}}$	0.55	0.05	0.05	0.53	0.05	0.05
NPP_{fineroot}	3.68	0.52	0.52	6.41	1.08	1.08
R_{leaf}	5.02	0.49	1.58	5.09	0.69	1.67
R_{stem}	8.71	1.07	2.82	8.46	1.24	2.82
$R_{\text{rhizosphere}}$	2.95	0.44	0.53	4.58	0.49	0.67
$R_{\text{coarseroot}}$	1.83	0.00	0.94	1.78	0.00	0.94
R_{soilhet}	11.35	1.34	1.75	12.17	1.31	1.79
R_{soil}	14.29	1.41	1.41	16.75	1.40	1.40
R_a	18.51	1.27	3.40	19.91	1.52	3.47
NPP	13.57	0.60	0.60	15.77	1.13	1.13
GPP	32.08	1.40	3.46	35.68	1.90	3.65
CUE	0.42	0.03	0.05	0.44	0.04	0.06

Units are all $\text{Mg C ha}^{-1} \text{ year}^{-1}$. Sample error is uncertainty associated with the spatial heterogeneity of the study plot 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.

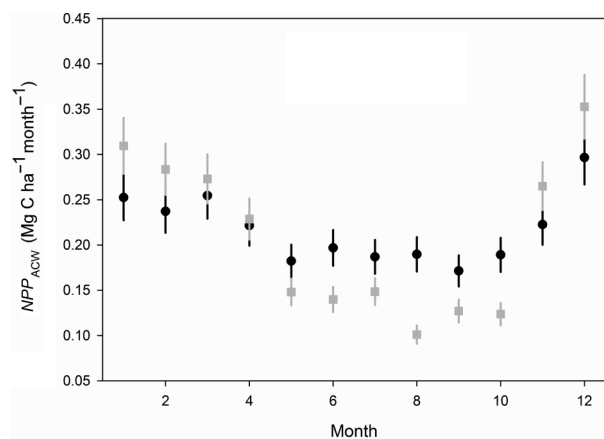


Figure 3. Above-ground woody NPP ($\text{Mg C ha}^{-1} \text{ month}^{-1}$) using dendrometer bands measured every one to three months for the tower plot (black circles) and the *terra preta* plot (grey squares) in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Error bars are the standard error assuming a 10% sampling error.

Canopy NPP

The tower plot samples indicated significantly ($P < 0.001$) greater leaf fall and reproductive litter than the *terra preta* plot, but twig fall was not significantly different between the two plots. At the *terra preta* plot there was a number of Brazil nut trees whose nuts were not accurately

accounted for in our calculations because they would tend to break the litter traps when they fell, or were collected and consumed by passers-by. We account for this by adding $1.0 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ to our total based on the number of productive trees and the average number and weight of fruits per tree (Aragao et al. 2009).

Total canopy NPP was estimated at $5.03 \pm 0.07 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ on the tower plot and $4.52 \pm 0.18 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ on the *terra preta* plot (Table 4) (including the Brazil nut correction). Leaves accounted for $3.21 \pm 0.06 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ on the tower plot and $2.63 \pm 0.16 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ on the *terra preta* plot. We estimated leaf herbivory to be $0.24 \pm 0.02 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at the tower plot and $0.21 \pm 0.01 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at the *terra preta* plot. The fraction of herbivory was greater at the *terra preta* plot ($7.1 \pm 1.1\%$ of leaf removed) plot than the tower plot ($6.4 \pm 1.0\%$ of leaf removed). There was a strong seasonality in leaf fall, with more leaves falling in the dry season (Figure 4). There was also a slight seasonality in reproductive material (fruits and flowers) with an increase in the dry season.

Total annual $NPP_{\text{branch turnover}}$ averaged $1.06 \pm 0.11 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at the tower plot and $1.10 \pm 0.11 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at the *terra preta* plot. $NPP_{\text{branch turnover}}$ was higher during the wet season and lower during the dry season (Figure 4). This is likely due to stronger wet season storms removing branches vs. any change in branch growth.

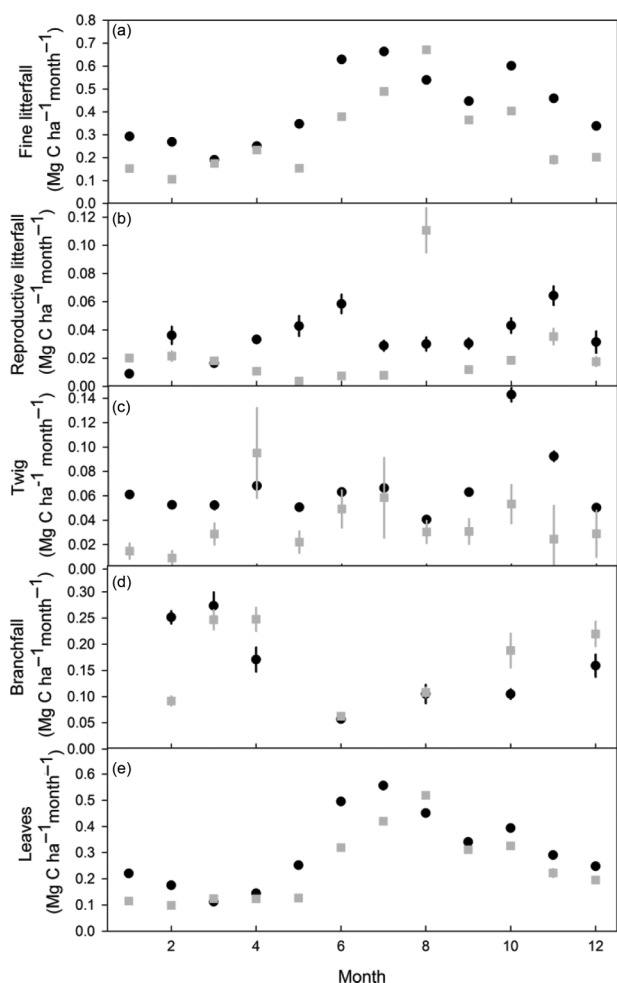


Figure 4. Monthly values from 25 litter traps of total (a) fine litterfall; (b) reproductive litter; (c) twig; (d) branch, and (e) leaf NPP ($\text{Mg C ha}^{-1} \text{ month}^{-1}$). Tower plot (black circles) and the *terra preta* plot (grey squares) in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Error bars are standard errors.

Soil respiration

Averaged monthly values of root respiration at the tower plot were 39% of soil respiration. This varied seasonally, with June to October values averaging 28% and the rest of the year averaging 44%. Averaged monthly values at the *terra preta* plot were 42% of soil respiration. There was less seasonality, with June to October values averaging 38% and the rest of the year averaging 44%.

Total soil respiration did not have a strong seasonal cycle but was slightly higher between May and September at both plots (Figure 5). Total annually averaged soil respiration was significantly lower ($P < 0.001$) at the tower plot vs. the *terra preta* plot ($14.29 \pm 1.41 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ vs. $16.75 \pm 1.40 \text{ Mg C ha}^{-1} \text{ year}^{-1}$).

Total rhizosphere respiration did not have a strong seasonal cycle but was slightly lower between May and September. Total annually averaged rhizosphere respiration was significantly lower ($P < 0.005$) at the tower plot vs. the *terra preta* plot ($2.95 \pm 0.53 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ vs. $4.58 \pm 0.67 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) (Table 4).

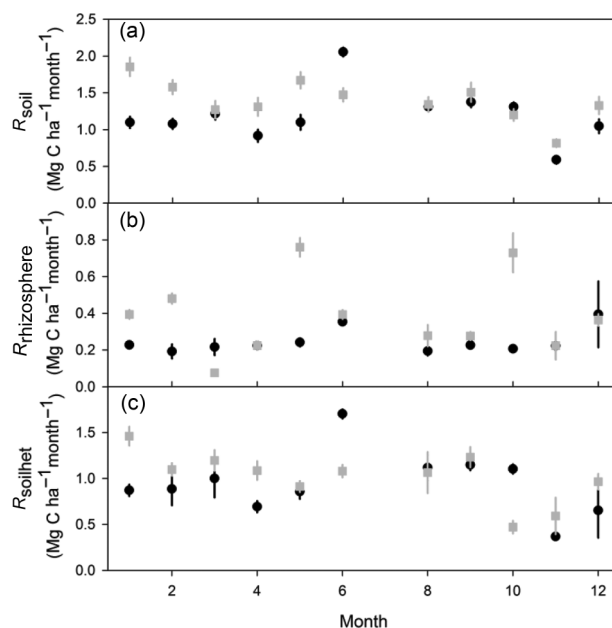


Figure 5. (a) Total soil respiration in units of $\text{Mg C ha}^{-1} \text{ month}^{-1}$ from 25 collars measured monthly. (b) rhizosphere respiration; (c) heterotrophic soil respiration. Tower plot (black circles) and the *terra preta* plot (grey squares) in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Error bars are standard errors.

Total heterotrophic soil respiration did not have a strong seasonal cycle but was slightly higher between May and September at both plots. Total annually averaged heterotrophic soil respiration was lower at the tower plot vs. the *terra preta* plot ($11.35 \pm 1.77 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ vs. $12.17 \pm 1.79 \text{ Mg C ha}^{-1} \text{ year}^{-1}$).

Wood respiration

Total above-ground woody surface area of large trees ($>10 \text{ cm}$ diameter) at the tower plot was estimated at $14,800 \text{ m}^2 \text{ ha}^{-1}$ and $14,400 \text{ m}^2 \text{ ha}^{-1}$ at the *terra preta* plot. Total woody surface area of small trees ($<10 \text{ cm}$ diameter) was $1710 \text{ m}^2 \text{ ha}^{-1}$ for the tower plot and $1920 \text{ m}^2 \text{ ha}^{-1}$ for the *terra preta* plot. Hence, we calculated a stem area index (SAI), which is the area of woody surface area per ground area, of 1.65 for the tower plot and 1.63 for the *terra preta* plot (Table 3).

Woody respiration per unit tree area was not significantly different between the plots ($2.08 \pm 0.15 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for the tower plot vs. $2.11 \pm 0.17 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for the *terra preta* plot).

To scale these measurements to the plot level, we first looked for a relationship between woody NPP and woody respiration of the 25 trees per plot on which measurements were made. The trees measured for woody respiration grew faster than the average trees in the plot. Therefore, when we scaled to the plot level, we reduced respiratory fluxes by 11% at the tower plot and by 7% at the *terra preta* plot.

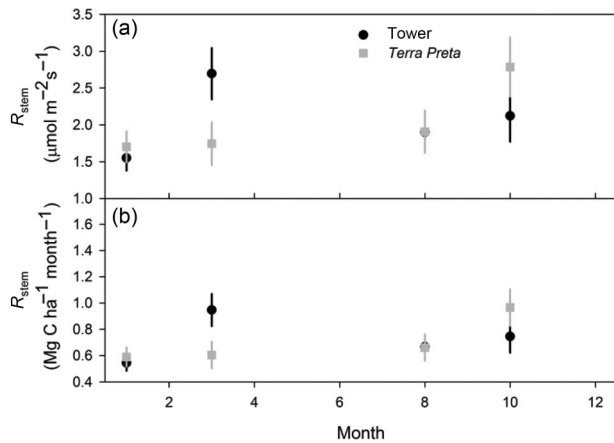


Figure 6. (a) Above-ground stem respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) from collars on 25 trees measured every three months; (b) multiplied by the total woody surface area of the plot ($\text{Mg C ha}^{-1} \text{ month}^{-1}$). Tower plot (black circles) and the *terra preta* plot (grey squares) in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Error bars are standard errors multiplied by woody surface area.

We then multiplied total plot woody surface area by our scaled woody respiration fluxes (Figure 6). Total estimated annual woody respiration was not significantly different and averaged $8.71 \pm 2.82 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at the tower plot and $8.46 \pm 2.82 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at the *terra preta* plot (Table 4).

Leaf respiration

Dark respiration of sun leaves was not significantly different between the plots ($0.43 \pm 0.02 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the tower plot and $0.41 \pm 0.03 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the *terra preta* plot), nor was dark respiration of shade leaves ($0.39 \pm 0.02 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the tower plot and $0.37 \pm 0.02 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the *terra preta* plot).

LAI was estimated at $5.0 \pm 0.19 \text{ m}^2 \text{ m}^{-2}$ at the tower plot and $5.3 \pm 0.21 \text{ m}^2 \text{ m}^{-2}$ at the *terra preta* plot. When we scaled our leaf-level respiration measurements by LAI, we estimated that total annual canopy respiration averaged $5.02 \pm 1.58 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at the tower plot and $5.09 \pm 1.67 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at the *terra preta* plot (Table 4).

Annual NPP, autotrophic respiration, GPP, and CUE

We summed annually averaged fine root NPP, woody NPP, branch NPP, canopy NPP, herbivory, and estimated coarse root NPP (21% of woody NPP) to estimate plot-level NPP for the tower plot at $13.57 \pm 0.60 \text{ Mg C ha}^{-1} \text{ year}^{-1}$, a value lower than that obtained for the *terra preta* plot ($15.77 \pm 1.13 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) (Figure 7). We summed annually averaged rhizosphere respiration, woody respiration, leaf respiration, and coarse root respiration to estimate that total autotrophic respiration was not very different between the tower plot and the *terra preta* plot ($18.51 \pm 3.40 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ vs. $19.91 \pm 3.47 \text{ Mg C ha}^{-1} \text{ year}^{-1}$). We added total autotrophic respiration to total NPP to estimate total

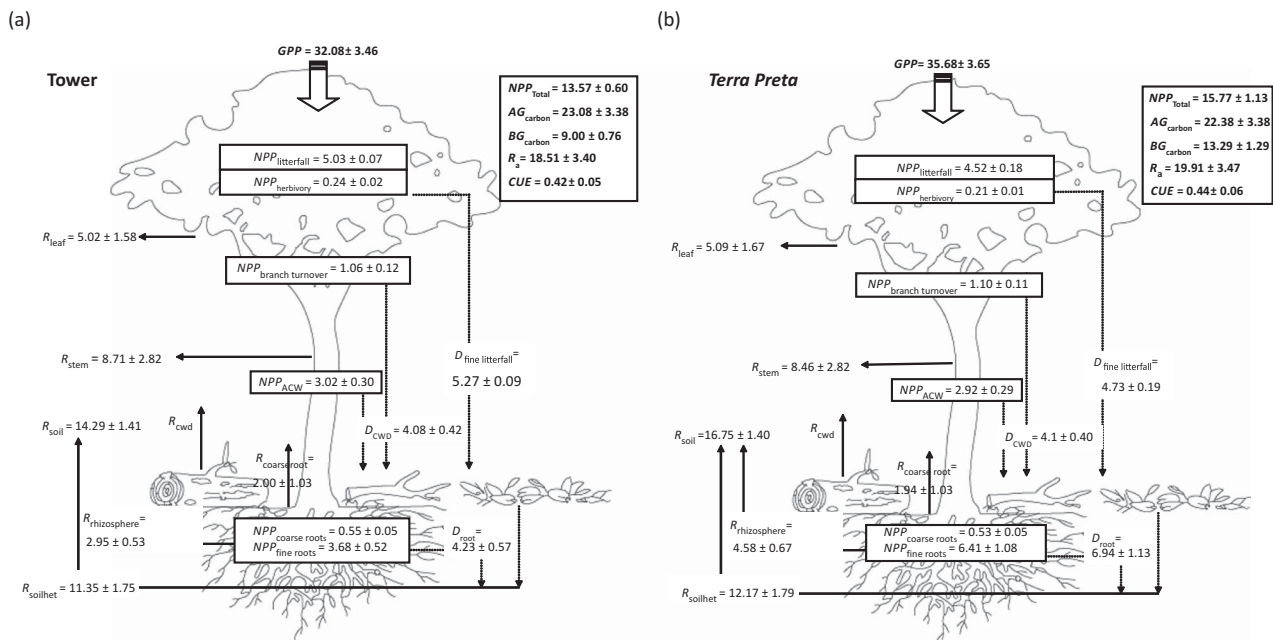


Figure 7. Diagram showing the magnitude and pattern of key carbon fluxes for (a) the tower plot; and (b) the *terra preta* plot in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Components with prefixes R , NPP and D denote respiration, net primary productivity and decomposition terms respectively. Detailed descriptions of C flux components measured are presented in Tables 1 and 2. All values are in units of $\text{Mg C ha}^{-1} \text{ year}^{-1}$, with the exception of carbon use efficiency (CUE) which is calculated as total NPP/GPP , 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.

GPP (for the tower plot $32.08 \pm 3.46 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ vs. $35.68 \pm 3.65 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for the *terra preta* plot). We divided total NPP by total GPP to estimate CUE and found that the tower plot was not very different from the *terra preta* plot (0.42 ± 0.05 vs. 0.44 ± 0.06) (Table 4).

Discussion

In addition to edaphic differences between the two plots, there were differences in microclimate, land use history (the *terra preta* plot was formerly an agroforestry site), and tree species composition. It is very difficult to definitively attribute ecological differences between the plots to soil, species, or climate. The differences in temperature and irradiance were relatively small between the two plots in comparison to the large edaphic differences, such as the almost five-fold higher concentration of phosphorus, a limiting nutrient in Amazonia, in the *terra preta* plot (see online supplemental material, Table S2), and we therefore attribute most of the differences to the *terra preta* soil type, although differing land use histories clearly played a role.

There were several significant differences in growth and respiration patterns between the two forests. Perhaps the clearest and most surprising result was the larger fine-root NPP and rhizosphere respiration at the *terra preta* plot vs. the tower plot. Many theoretical studies of NPP allocation in trees (Bloom et al. 1985) would have predicted lesser root growth in the forests growing in the more nutrient-rich *terra preta* soils. Carbon allocated to root growth was not greater at the *terra preta* plot simply because of greater total NPP, and there was a clear increase in NPP allocation at the *terra preta* plot towards root growth (41% vs. 27% in the tower plot (Table 5)). These allocation patterns compare to mean allocation of fine roots in tropical forests of $27 \pm 11\%$ (Malhi et al. 2011). Greater carbon may also have been allocated towards the roots in the *terra*

Table 5. Patterns of carbon allocation for above-ground (AG) and below-ground (BG) components, NPP allocation, and partitioning of autotrophic respiration for the tower plot and *terra preta* plot in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil.

	Tower		<i>Terra preta</i>	
	Mean	SE	Mean	SE
Total carbon allocation				
AG carbon ($\text{Mg C ha}^{-1} \text{ year}^{-1}$)	23.08	3.38	22.38	3.42
BG carbon ($\text{Mg C ha}^{-1} \text{ year}^{-1}$)	9.00	0.76	13.29	1.29
AG fraction (%)	0.72	0.05	0.63	0.06
BG fraction (%)	0.28	0.03	0.37	0.04
Allocation of NPP				
Canopy (%)	0.39	0.02	0.30	0.03
Wood (%)	0.34	0.07	0.29	0.06
Fine roots (%)	0.27	0.04	0.41	0.07
Partitioning of autotrophic respiration				
Canopy (%)	0.27	0.03	0.26	0.04
Wood (%)	0.57	0.09	0.51	0.09
Rhizosphere (%)	0.16	0.03	0.23	0.03

preta plot not because of differences in nutrient concentrations but because the secondary forest was far from mature and the additional root growth provides nutrients key for a still-expanding forest.

NPP_{ACW} was similar at the *terra preta* plot and the tower plot. Individual trees in the *terra preta* plot grew at a faster rate than in the tower, plot with average circumference expanding by 4.6 cm at the *terra preta* plot vs. 2.0 cm over a six-year period (2005–2010). However, wood density and average tree height was lower, perhaps a legacy of the agroforestry history of this plot, which reduced the difference in total woody NPP.

We also found significant seasonality in all of the NPP measurements at both the tower and *terra preta* plots. Wood and root NPP peaked in the wet season while litterfall peaked in the dry season. This is likely to be related to the strong seasonality in climate, with the dry period corresponding to periods of increased solar radiation that have been associated with leaf flush in nearby forests (Doughty and Goulden 2008) (Figure 1). The seasonality in the NPP measurements was matched by a smaller seasonality in autotrophic respiration.

Some aspects of the carbon cycle in the *terra preta* plot are more similar to fertile western Amazonian forests than to the surrounding nutrient-poor eastern Amazonian forests. For example, both the *terra preta* plot and western Amazonian forests tend to have lower wood density (Baker et al. 2004) and higher herbivory fractions than eastern Amazonian forests (D.B. Metcalfe, pers. comm.). Fertile soils may allow rapid tree growth, which favours species with low wood density, and more nutritious leaves may encourage increased herbivory. However, an alternative explanation for the low wood density is the disturbance in the *terra preta* plot leading to more gaps and increased low-wood density pioneer species.

Total GPP was $32.08 \pm 3.46 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at the tower plot and $35.68 \pm 3.65 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at the *terra preta* plot. Much of this increased productivity was allocated into the rhizosphere, which was ca. $3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ greater in the *terra preta* plot. A previous study found an NPP of $17.0 \pm 1.41 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at the *terra preta* plot (Aragao et al. 2009), which is greater than our current estimate of NPP at $15.77 \pm 1.13 \text{ Mg C ha}^{-1} \text{ year}^{-1}$. The difference may result from a greater amount of data included in this study and from inter-annual differences. A previous study also measured GPP at the tower plot using the eddy covariance method, and found an average GPP of $36.3 \pm 2.0 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (Carswell et al. 2002), which is slightly higher than our current GPP estimate of $32.08 \pm 3.46 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ and a previous ‘bottom up’ estimate for the site at $34.4 \pm 4.2 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (Malhi et al. 2009). Malhi et al. (2009) found a total autotrophic respiration rate of $21.4 \pm 4.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (compared to our current value of $18.51 \pm 3.40 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) and an NPP of $10.0 \pm 1.2 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (compared to our current value of $13.57 \pm 0.60 \text{ Mg C ha}^{-1} \text{ year}^{-1}$). Our NPP values may be slightly higher

due to the contribution of additional carbon sources, such as coarse-root NPP, respiration, and herbivory.

We assigned additional error to canopy and wood respiration (30%) that had a great deal of uncertainty associated with scaling (Tables 2 and 4). For instance, branch respiration per unit surface area may be higher than bole respiration per unit surface area (Cavaleri et al. 2006) but this may be offset by soil CO₂ in the transpiration stream affecting the stem CO₂ efflux measurements. The scaling of leaf respiration to total canopy respiration is equally prone to large scaling uncertainty, due to the conversion to day respiration, the multiplication by LAI, and the sparseness of the measurements. Although there is large uncertainty in each scaling term, it is unlikely that a large bias occurs in one direction. However, since our measured GPP was less than that measured by the eddy covariance tower (although within the total error estimate), our scaling may indicate a slight low bias. $NPP_{\text{branch turnover}}$ is another source of uncertainty as branch fall is inherently more stochastic than the growth of new branches. However, since we have collected several years of data, this stochasticity should have been reduced.

The *terra preta* plot had a CUE of 0.44 ± 0.06 compared to 0.42 ± 0.05 at the tower plot. Previous studies have found a CUE of ca. 0.3 for undisturbed old-growth tropical forests (Chambers et al. 2004; Malhi et al. 2009). The slightly higher CUE at the *terra preta* plot may be due to the different species present or an agroforestry ‘disturbance’ in the recent past, which led the forest to allocate more of its carbon towards growth. Alternatively, the higher CUE at the *terra preta* plot may be due natural higher dynamism due to a decreased mean residence time of the trees at the plot.

The *terra preta* plot had slightly higher productivity, of which it allocated slightly more of the carbon towards growth, leading to greater NPP than the tower plot. Of this increased NPP, more carbon was allocated towards roots vs. wood or leaves. This may increase the carbon content of an already carbon-rich soil over long periods of time. However, heterotrophic soil respiration was also higher at the *terra preta* plot, which indicated increased decomposition. Fine root NPP increased by ca. 3 Mg C ha⁻¹ year⁻¹ and heterotrophic soil respiration increased by ca. 1 Mg C ha⁻¹ year⁻¹, indicating a possible slight increase in long-term soil carbon storage over the two-year period of the study.

Conclusion

Our results showed that trees on the *terra preta* soil type had greater NPP and allocated more of that NPP towards root growth. This increased allocation of NPP towards root growth is remarkable for two reasons. Firstly, it contradicts the predictions of resource-allocation theory. Secondly, the increased root growth has the ability to further enhance carbon stocks in the already carbon-rich soil. However, increased heterotrophic soil respiration partially offset this potential increased source of soil carbon. Overall, this study

offers the first long-term glimpse of the complete carbon cycle in a tropical forest growing on the *terra preta* soil type.

Acknowledgements

This work is a product of the RAINFOR consortium and a component site of the GEM (Global Ecosystems Monitoring) network. It was funded by a grant from the Gordon and Betty Moore Foundation to the Amazon Forest Inventory Network (RAINFOR), and a grant to YM from the UK Natural Environment Research Council (Grants NE/D014174/1). YM is supported by the Jackson Foundation. We thank the Museu Paraense Emilio Goeldi and their Ferreira Penna Scientific Field Station at Caxiuana for invaluable field support. We dedicate this paper to the memory of our co-author Samuel Almeida, who was so instrumental and enthusiastic in establishing this study and selecting the study plot.

Notes on contributors

Christopher E. Doughty is a lecturer in ecosystem ecology. His main research interest lies in understanding tropical forest dynamics and biogeochemical cycling.

Daniel B. Metcalfe is an assistant professor in forest ecology & management. His research focuses on issues intersecting ecophysiology, soil science and silviculture.

Mauricio C. da Costa, Luiz E.O.C. Aragão, Kate Halladay, Carlos A. Quesada, João A. Silva, Alex A.R. de Oliveira and G.F.C. Neto are tropical forest ecologists who all contributed data to this study.

Samuel S. Almeida (deceased), was a professor who specialised in the ecology and taxonomy of tropical flora.

Cecile A.J. Girardin is an ecosystems scientist who focuses on carbon cycling in tropical forest ecosystems.

Anthony C.L. da Costa is a professor in Belem, Brazil who studies the effect of drought on tropical forests.

Yadvinder Malhi is a professor in ecosystem science. His research interests focuses on interactions between forest ecosystems and the global atmosphere, with a particular focus on their role in global carbon, energy and water cycles.

References

- Aragao LEOC, Malhi Y, Metcalfe DB, Silva-Espejo JE, Jimenez E, Navarrete D, Almeida S, Costa ACL, Salinas N, Phillips OL, et al. 2009. Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences* 6:2759–2778.
- Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen TJ, Laurance SG, Laurance WF, et al. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology* 10:545–562.
- Bloom AJ, Chapin FS, Mooney HA. 1985. Resource limitation in plants – an economic analogy. *Annual Review of Ecology and Systematics* 16:363–392.
- Cairns MA, Brown S, Helmer EH, Baumgardner GA. 1997. Root biomass allocation in the world’s upland forests. *Oecologia* 111:1–11.
- Carswell FE, Costa AL, Palheta M, Malhi Y, Meir P, Costa JDR, Ruivo MD, Leal LDM, Costa JMN, Clement RJ, et al. 2002. Seasonality in CO₂ and H₂O flux at an eastern Amazonian

- rain forest. *Journal of Geophysical Research – Atmospheres* 107(D20). doi:10.1029/2000JD000284, 2002.
- Cavaleri MA, Oberbauer SF, Ryan MG. 2006. Wood CO₂ efflux in a primary tropical rain forest. *Global Change Biology* 12:2442–2458.
- Chambers JQ, Tribuzy ES, Toledo LC, Crispim BF, Higuchi N, dos Santos J, Araujo AC, Kruijt B, Nobre AD, Trumbore SE. 2004. Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecological Applications* 14:S72–S88.
- Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Folster H, Fromard F, Higuchi N, Kira T, et al. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145:87–99.
- Demarez V, Duthoit S, Baret F, Weiss M, Dedieu G. 2008. Estimation of leaf area and clumping indexes of crops with hemispherical photographs. *Agricultural and Forest Meteorology* 148:644–655.
- Denevan WM. 2001. *Cultivated landscapes of native Amazonia and the Andes*. Oxford: Oxford University Press.
- Doughty CE, Goulden ML. 2008. Seasonal patterns of tropical forest leaf area index and CO₂ exchange. *Journal of Geophysical Research–Biogeosciences* 113.
- Galbraith D, da Costa ACL, Portela BTT, Levy PWM, Fisher RA, Meir P. In review 2013. Effect of imposed drought on root biomass and its distribution with depth in an Amazonian rainforest. *Global Change Biology*.
- Girardin CAJ, Malhi Y, Aragao LEOC, Mamani M, Huasco WH, Durand L, Feeley KJ, Rapp J, Silva-Espejo JE, Silman M, et al. 2010. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology* 16:3176–3192.
- Glaser B, Haumaier L, Guggenberger G, Zech W. 1999. Black carbon in terra preta and oxisols of the Brazilian Amazon as estimated by benzenecarboxylic acids as specific markers. *Abstracts of Papers of the American Chemical Society* 217:U829–U829.
- Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108:389–411.
- Lehmann J, Kern DC, Glaser B, Woods WI. 2003. *Amazonian dark earths: origin, properties, management*. Dordrecht (the Netherlands): Kluwer Academic Publishers.
- Malhi Y, Aragao LEOC, Metcalfe DB, Paiva R, Quesada CA, Almeida S, Anderson L, Brando P, Chambers JQ, da Costa ACL, et al. 2009. Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology* 15:1255–1274.
- Malhi Y, Baker TR, Phillips OL, Almeida S, Alvarez E, Arroyo L, Chave J, Czimczik CI, Di Fiore A, Higuchi N, et al. 2004. The above-ground coarse wood productivity of 104 neotropical forest plots. *Global Change Biology* 10:563–591.
- Malhi Y, Doughty C, Galbraith D. 2011. The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society B – Biological Sciences* 366:3225–3245.
- Malhi Y, Wood D, Baker TR, Wright J, Phillips OL, Cochrane T, Meir P, Chave J, Almeida S, Arroyo L, et al. 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology* 12:1107–1138.
- Martin AR, Thomas SC. 2011. A reassessment of carbon content in tropical trees. *PLoS ONE* 6(8):e23533. doi:10.1371/journal.pone.0023533
- McMichael CH, Piperno DR, Bush MB, Silman MR, Zimmerman AR, Raczka MF, Lobato LC. 2012. Sparse pre-Columbian human habitation in western Amazonia. *Science* 336:1429–1431.
- Meggers B. 1971. *Amazonia: man and culture in a counterfeit paradise*. Harlan Davidson. Washington (DC): Smithsonian Institution Scholarly Press.
- Metcalfe DB, Meir P, Aragao LEOC, Malhi Y, da Costa ACL, Braga A, Goncalves PHL, de Athaydes J, de Almeida SS, Williams M. 2007. Factors controlling spatio-temporal variation in carbon dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the eastern Amazon. *Journal of Geophysical Research–Biogeosciences* 112. doi:10.1029/2007JG000443.
- Quesada CA, Lloyd J, Anderson LO, Fyllas NM, Schwarz M, Czimczik CI. 2011. Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences* 8:1415–1440.
- Quesada CA, Lloyd J, Schwarz M, Patino S, Baker TR, Czimczik C, Fyllas NM, Martinelli L, Nardoto GB, Schmerler J, et al. 2010. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences* 7:1515–1541.
- Reich PB, Walters MB, Ellsworth DS, Vose JM, Volin JL, Gresham CA, Bowman WD. 1998. Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia* 114:471–482.
- Roosevelt AC. 1993. The rise and fall of the Amazon chiefdoms. *Homme* 33:255–283.
- Smith J, van de Kop P, Reategui K, Lombardi I, Sabogal C, Diaz A. 1999. Dynamics of secondary forests in slash-and-burn farming: interactions among land use types in the Peruvian Amazon. *Agriculture Ecosystems & Environment* 76:85–98.
- Smith NJH. 1980. Anthrosols and human carrying-capacity in Amazonia. *Annals of the Association of American Geographers* 70:553–566.
- Wolf D, Amonette JE, Street-Perrott FA, Lehmann J, Joseph S. 2010. Sustainable biochar to mitigate global climate change. *Nature Communications* 1:56. doi:10.1038/ncomms1053.