Ecosystem productivity and carbon cycling in intact and annually burnt forest at the dry southern limit of the Amazon rainforest (Mato Grosso, Brazil)

Wanderley Rocha[ab], Daniel B. Metcalfe[c], Chris E. Doughty[d], Paulo Brando[ab], Divino Silvério[a], Kate Halladay[d], Daniel C. Nepstad[a], Jennifer K. Balch[e] & Yadvinder Malhi[d]

[a] Amazon Environmental Research Institute (IPAM), Canarana, Mato Grosso, Brazil

[b] Universidade do Estado do Mato Grosso, Novo Xavantina, Mato Grosso, Brazil

[c] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

[d] Environmental Change Institute, School of Geography and the Environment, University of Oxford, UK

[e] Department of Geography, Penn State University, Pennsylvania, USA
Published online: 18 Sep 2013.

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis
Taylor & Francis Group

Ecosystem productivity and carbon cycling in intact and annually burnt forest at the dry southern limit of the Amazon rainforest (Mato Grosso, Brazil)

Wanderley Rocha[a,b], Daniel B. Metcalfe[c]*, Chris E. Doughty[d], Paulo Brando[a,b], Divino Silvério[a], Kate Halladay[d], Daniel C. Nepstad[a], Jennifer K. Balch[e] and Yadvinder Malhi[d]*

[a]*Amazon Environmental Research Institute (IPAM), Canarana, Mato Grosso, Brazil;* [b]*Universidade do Estado do Mato Grosso, Novo Xavantina, Mato Grosso, Brazil;* [c]*Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden;* [d]*Environmental Change Institute, School of Geography and the Environment, University of Oxford, UK;* [e]*Department of Geography, Penn State University, Pennsylvania, USA*

Background: The impact of fire on carbon cycling in tropical forests is potentially large, but remains poorly quantified, particularly in the locality of the transition forests that mark the boundaries between humid forests and savannas.

Aims: To present the first comprehensive description of the impact of repeated low intensity, understorey fire on carbon cycling in a semi-deciduous, seasonally dry tropical forest on infertile soil in south-eastern Amazonia.

Methods: We compared an annually burnt forest plot with a control plot over a three-year period (2009–2011). For each plot we quantified the components of net primary productivity (NPP), autotrophic (R_a) and heterotrophic respiration (R_h), and estimated total plant carbon expenditure (PCE, the sum of NPP and R_a) and carbon-use efficiency (CUE, the quotient of NPP/PCE).

Results: Total NPP and R_a were 15 and 4% lower on the burnt plot than on the control, respectively. Both plots were characterised by a slightly higher CUE of 0.36–0.39, compared to evergreen lowland Amazon forests.

Conclusions: These measurements provide the first evidence of a distinctive pattern of carbon cycling within this transitional forest. Overall, regular understorey fire is shown to have little impact on ecosystem-level carbon fluxes.

Keywords: allocation; carbon cycling; CUE; fire experiment; GPP; NPP; Tanguro; tropical seasonally dry rainforest

Introduction

The Amazon forests store ca. 120 petagrams (1 Pg = 1×10^9 tonnes) of carbon (C) and contribute 10% of global net biomass production (Melillo et al. 1996; Malhi and Grace 2000), influencing both the regional and the global climate. However, climate change can drastically alter the ability of these forests to store C. Droughts can affect the Amazon C cycle not only by killing trees and reducing tree growth, but also by increasing the intensity and extension of forest fires (Alencar et al. 2006). During the drought of 1998, for instance, the area burnt in the Brazilian Amazon was ca. 39,000 km², much larger than the 17,384 km² deforested directly (Nepstad et al. 2001; Alencar et al. 2004, 2006), emitting significant amounts of C into the atmosphere (Aragão and Shimabukuro 2010). Natural forest fires are a very rare occurrence across most of the Amazon rainforest (Hammond and ter Steege 1998; Turcq et al. 1998; Behling et al. 2001; Bush et al. 2004). However, after large-scale human colonisation commenced, the frequency and severity of fire events increased across the region, primarily through accidental spread from fires intentionally set to prepare land for agriculture (Cochrane et al. 1999; Nepstad et al. 1999). In the Amazon the rate of forest degradation due to accidental fires can often exceed degradation caused by logging (Alencar et al. 2006). This has been exacerbated by the increased susceptibility to

fire of degraded and logged forests; these have become more widespread in the Amazon, and the rise in the frequency of severe drought is often, although not always, associated with El Niño events (Laurance and Williamson 2001; Nepstad et al. 2004; Aragão et al. 2007; Cochrane and Laurance 2008). Thus, where in close proximity to human settlements high levels of forest disturbance and dry conditions overlap, the resultant fires can have a particularly severe impact on forest structure and function, and can release large quantities of carbon dioxide (CO_2) into the atmosphere (Potter et al. 2002, 2009; van der Werf 2003).

Studies of fire-associated forest CO_2 release have tended to focus on the most immediate, visible and direct fluxes from combustion of above-ground organic material (e.g. Kauffman et al. 1998; Haugaasen et al. 2003; Balch et al. 2008; Potter et al. 2009). However, much of the tropical forest C is stored below-ground as a complex and spatially heterogeneous mixture of different substances (plant roots, mycorrhizae, dead organic matter and organic compounds in mineral soil) each with their own sensitivity to various environmental factors. Therefore, understanding and predicting the impact of fire on the flow of CO_2 from these different components, and their net effect on overall soil CO_2 efflux, is critical to accurately estimating the impact of fire on the tropical forest C balance. Moreover, in

*Corresponding authors. Email: dbmetcalfe@gmail.com; yadvinder.malhi@ouce.ox.ac.uk

order to understand and model the response of ecosystem productivity and biomass to fire and drought it is important to gain a comprehensive understanding of the complete C cycle, including production, respiration, allocation and turnover, of which the biomass and soil C stores are components. These components are required in order to estimate the stability of stored C, as the long-term outcome of the balance between C assimilated by photosynthesis (gross primary productivity, GPP) and C released via autotrophic (R_a) and heterotrophic respiration (R_h) (Chapin et al. 2006). In this context, a key parameter is the carbon use efficiency (CUE) of the forest, which is the proportion of GPP used for net primary production of biomass (NPP) over relatively long turnover times, rather than the rapid metabolism of photosynthate to support R_a (DeLucia et al. 2007). Such a comprehensive understanding is beginning to emerge for a few sites in humid Amazonian forests (Chambers et al. 2004; Malhi et al. 2009a; Metcalfe et al. 2010), but no such study has previously been conducted in a seasonally dry tropical forest.

The Amazonian forest formations with greatest susceptibility to fire are the transitional forests, such as those located at the dry southern extremity of Amazonia (Nepstad et al. 1999; Alencar et al. 2005), which also demarcates the Brazilian agricultural frontier. This is one of the tropical forest regions most likely to become drier as a result of global climate change (Zelazowski et al. 2011). Yet despite their susceptibility to drought and fire, the transition forests remain poorly studied. To address this gap in knowledge, a large-scale burn experiment was initiated in 2004 to examine the effect of low intensity understorey fire on ecosystem structure and function in this threatened ecotone (Balch et al. 2008). By the start of our study in 2009 the 0.5×1.0 km experimental burn plot had been subjected to six ground surface fires in the previous eight years. In the present study we present a comprehensive picture of forest C cycling across a full seasonal cycle, averaged over 2009–2011 in the experimentally burnt forest, and compare these measurements with matching data from a similar, but unmodified, control plot nearby. The specific questions we ask are as follows:

(1) How do the components of NPP vary over the seasonal cycle in the burned and control plots?
(2) How do the components of R_a and R_h vary over the seasonal cycle in these two plots?
(3) What is the NPP, CUE and biomass allocation in this seasonally dry transition forest, how do these differ from wetter Amazon forests, and how do they change following regular burning?

Materials and methods

Study site and experimental design

The study area was located on the Fazenda Tanguro (ca. 80,000 ha) in Mato Grosso State (Figure 1), ca. 30 km north of the southern boundary of the Amazon rainforest in Brazil (13°04′ 35.39′ S, 52°23′ 08.85′ W). The average annual rainfall was ca. 1770 mm (2005–2011), with a very intense dry season, and monthly rainfall between the months of May and August typically below 10 mm (Figure 2).

The average annual air temperature was 25°C, with usually less than 5°C seasonal variation around this mean. The soil type at the site was a red-yellow alic dystrophic latosol (RADAM Brasil 1974; Brazilian soil classification), a relatively infertile sandy ferralsol (FAO classification) or oxisol (Haplustox; US Department of Agriculture classification scheme); the groundwater was at a depth of ca. 15 m, and no layers of soil were able to prevent root penetration through the soil profile. These soils are among the least fertile in Amazonia and are widespread across eastern Amazonia (Quesada et al. 2010). The study was located within a residual tract of transitional forest kept as a protected reserve by the landowner, as required by Brazilian law. The forest type according to the Veloso et al. (1991) classification scheme was seasonal semi-deciduous alluvial.

The forest had a relatively low mean canopy height (20 m) and low plant species diversity in comparison with the wetter forests typical of the central Amazon (97 species of trees and lianas ≥10 cm diameter at 1.3 m stem height above the ground (dbh) identified over the entire 150 ha experimental area) (Balch et al. 2011. The 10 most common species accounted for ca. 50% of the Vegetation Importance Index: *Amaioua guianensis* Aubl. (7.8%), *Ocotea acutangula* (Miq.) Mez (7.5%), *Aspidosperma excelsum* Benth. (6.4%), *Ocotea guianensis* Aubl. (6.2%), *Tapirira guianensis* Aubl. (5.9), *Micropholis egensis* (A. DC.) Pierre (4.4%), *Trattinnickia burserifolia* Mart. (4.1%), *Sloanea eichleri* K. Schum. (4.0%), *Trattinnickia rhoifolia* Willd. (3.7%), and *Pouteria ramiflora* (Mart.) Radlk. (3.6%) (Balch et al. 2008). In addition, at least 23 forest species co-occurred in the savanna (cerrado) biome which adjoins the forest ca. 30 km to the south of the study area.

A burning experiment was established within a 1.5×1.0 km^2 (150 ha) area of the property's legally protected forest reserve to identify the effect of fires on forest vegetation structure and its rate of recovery after the fire. The site was situated within the forest at the edge of a pasture area (now an area of soybean cultivation with no fire use). The site had no known logging or previous fires in the recent past, or at least for several decades. The study design and effect of the burning experiment on microclimate and forest structure have been described in detail by Balch et al. (2008), and mortality patterns and species–fire interactions described by Balch et al. (2011) and Brando et al. (2012), respectively.

In 2004 the experimental area was divided into three adjacent treatment areas, each of 50 ha (0.5×1.0 km^2) (Figure 1). In two of the treatment areas, fires were set with kerosene drip torches along transects spaced 50 m apart, within two areas of previously undisturbed forest. Fires were set during three or four consecutive days between 9:00 and 16:00; 10 km of fire lines were set up per 50 ha plot. The majority of fires became extinguished naturally by nightfall and were then relit on subsequent days. This method achieved a low-intensity, slow-moving fire across
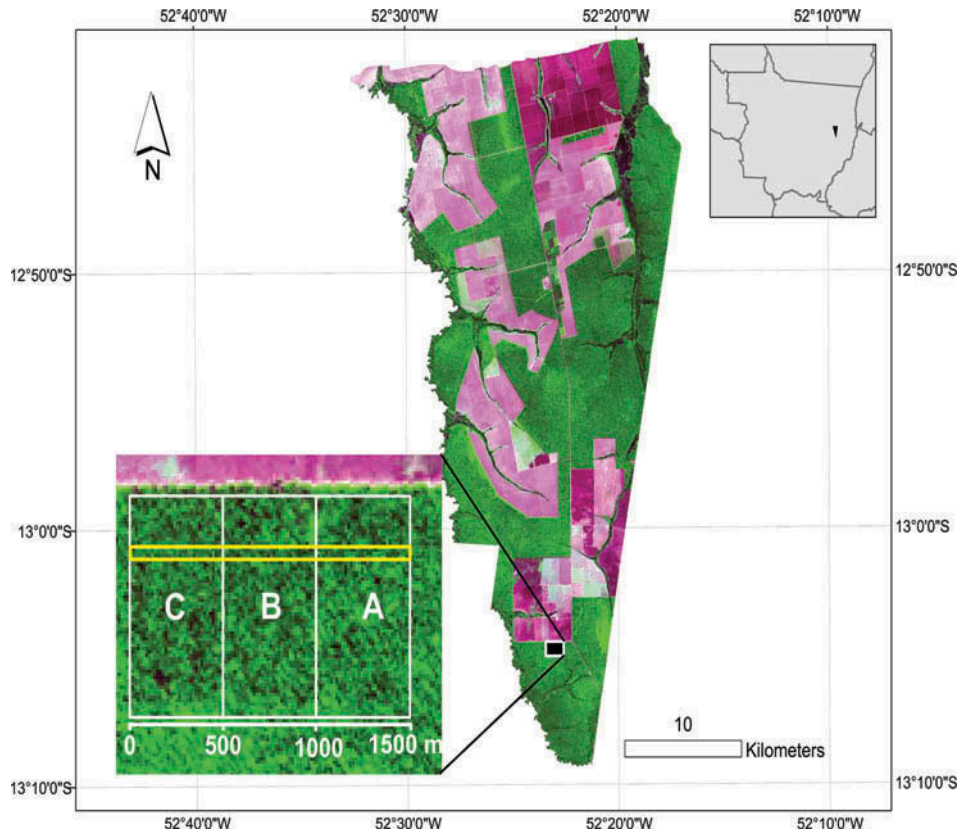
Figure 1.   Location of the experimental area, Fazenda Tanguro, in Mato Grosso State, Brazil (upper right panel insert). Colouring indicates vegetation density (high, green; low, pink/purple). The control plot is A, the 3-year burn (not studied here) is B, and the annually burnt plot, the burn treatment plot featured in the present study, is C.

the plot, typical of naturally occurring tropical understorey forest fires. The fire was carefully controlled along the plot margin to prevent it spreading into nearby forest, including the third treatment area, which was unmodified, old-growth forest chosen as a control plot. This process was repeated every year in one treatment (burn plot) near the end of the dry season, when most wild fires occur in the region. In two years (2008 and 2011) restrictions prevented burning, so the burn treatment had been applied six times by the end of the present study.

The second burn treatment, in which the forest was burned every three years, was not the focus of our measurements. Prior to the first fire, extensive vegetation surveys indicated that the control and burn plots had similar tree species diversity (68 and 82 on the control and burn plots, respectively) and composition, and similar overall density (2200 and 2246 stems ≥10 cm dbh) and size distribution of stems (Balch et al. 2008, 2011). After the third burn in 2006, near-soil air conditions became warmer and drier (Balch et al. 2008; Silveira et al. 2009), fine ground surface litter became 38% drier, and its mass was reduced by 13% compared to the control plot. Over the same period the mortality of trees and lianas ≥10 cm dbh on the burn plot increased by 96% relative to the control (Balch et al. 2011), associated with a 22% reduction in canopy density measured in terms of leaf area index (LAI). Within the 50 ha treatments, we focused the measurements reported here on

a 1-ha plot of 500×20 m^2 along a transect (F-transect) located 250 m from (and running parallel to) the edge of the forest.

The substantial logistical and financial costs of maintaining the burning treatment precluded further replication outside the experimental area, but the study provided an insight into the effects of an important natural phenomenon on an ecologically meaningful spatial scale that would have been impossible to gather from smaller scale, more easily replicated experiments (Carpenter 1996; Sullivan 1997; Osmond et al. 2004; Stokstad 2005). Fire events are increasing in frequency across the Amazon (Alencar et al. 2006; Aragão and Shimabukuro 2010), particularly in fragmented forests which have burned previously (Cochrane and Schulze 1999; Cochrane 2001). The burn treatments therefore represent an extreme but plausible natural state for a significant portion of Amazon forest facing a drier future climate with more extensive agricultural land-use (Nepstad et al. 2001; Cardoso et al. 2003).

Meteorological data

Solar radiation, air temperature, relative humidity and precipitation time series were collected from an automatic weather station located in open ground near the study plots (13.08°S, 51.48°W). The original data were measured at hourly resolution for the period January 2004 to
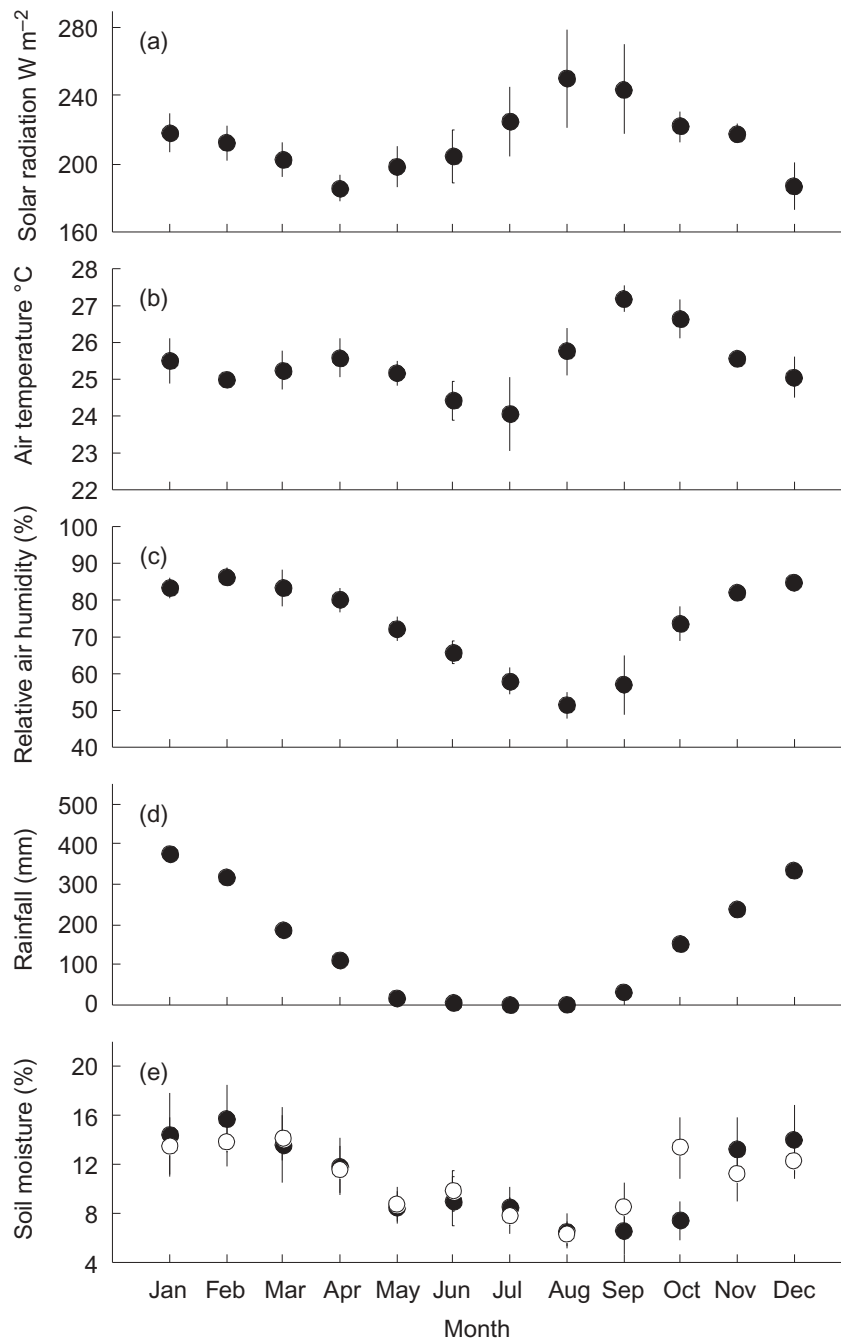
Figure 2.   Seasonal climate data for (a) total radiation, (b) average monthly temperature, (c) relative atmospheric humidity, (d) average monthly precipitation and (e) surface soil volumetric moisture, in Fazenda Tanguro, Mato Grosso State, Brazil. All variables were recorded using a meteorological station situated in open ground near the study plots, with the exception of soil moisture which was recorded by sensors installed in the control and annual burn plots. Error bars are standard errors over multiple years, to give an indication of inter-annual variability. Filled circle, control; open circle, burn.

December 2011. During control of temperature, values ≥4 standard deviations from the mean were discarded, as were relative humidity values ≥100%, and precipitation values ≥100 mm over 30 min. In the generation of a monthly time series for each variable, at least 90% of the maximum possible values during a given month had to be present for that month to be included in the time series. For solar radiation, temperature and relative humidity, the monthly mean value for each missing month was used to add the missing values. In the case of precipitation,

only months in which all the days were sampled were considered.

The precipitation monthly time series was gap-filled using data from a nearby station, which is part of the Hidroweb network (station number 01352001), located at 13.50°S, 52.45°W. These data were available hourly but were aggregated to generate a monthly time series. Surface soil moisture was recorded using probes installed in each plot. Maximum climatological water deficit (MCWD), a climatological measure of tropical forest water stress, was

calculated using the gap-filled monthly time series for precipitation, according to the equations listed by Aragão et al. (2007).

Carbon fluxes

The protocols used to estimate the ecosystem C flux components were largely based on those developed by the RAINFOR–GEM network. A detailed description is available online for the download (http://gem.tropicalforests.ox.ac.uk) and is given 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:

$$NPP_{AG} = NPP_{ACW} + NPP_{Litter\ fall}$$
$$+ NPP_{Branch\ turnover} - NPP_{Herbivory} \quad (1)$$

$$NPP_{BG} = NPP_{Fine\ roots} + NPP_{Coarse\ roots} \quad (2)$$

This neglects several small NPP terms, such as the NPP lost as volatile organic emissions, and litter decomposed in the canopy or shed by ground flora below the litter traps. Total R_a was estimated as

$$R_a = R_{Leaves} + R_{Stems} + R_{Rhizosphere} + R_{Coarse\ roots} \quad (3)$$

Here we consider root exudates and transfer to mycorrhizae to be a component of $R_{Rhizosphere}$ rather than NPP. In quasi-steady state conditions (and on annual timescales or longer where there are no net changes in plant non-structural carbohydrate storage), GPP should be approximately equal to PCE. Hence, we estimated GPP on the control plot as

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

In perturbed systems such as the burn plot, plant-level steady-state conditions may not apply. Thus, we interpret the sum of NPP and R_a in the burn plot as PCE (Metcalfe et al. 2010). Using these data, we can estimate the CUE as the proportion of total GPP/PCE invested in total NPP:

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

Statistics and error analysis

A repeated-measures analysis of variance (ANOVA) was used to test for significant seasonal shifts in ecosystem C components between plots. In addition, mean annual differences between the two plots were assessed using a student's t-test, assuming that the component measurements within each treatment were independent replicates.

All the estimated fluxes reported in this study are in Mg C ha^{-1} year^{-1}, and all reported errors show ±1 SE.

Errors were propagated by quadrature of absolute errors for addition and subtraction, and quadrature of relative errors for division and multiplication (Taylor et al. 1997; Malhi et al. 2009a). This assumes that uncertainties were independent and normally distributed. We explicitly consider two distinct types of uncertainty in this study, firstly, the sampling error associated with spatial variation in the variables measured, and secondly, the measurement uncertainty due to equipment functioning, measurement accuracy, and in particular scaling localised measurements to whole-tree and whole-plot estimates. Here we assume that most NPP terms are measured relatively precisely and sampled without large biases, and NPP error was thus largely the result of sampling uncertainty. In contrast, we believe that the main R_a terms included a large measurement uncertainty, though this is very difficult to quantify. The approach taken here is to assign explicit and conservative estimates of the measurement uncertainty for these components, as summarised in Tables 1 and 2. Some components were not directly measured at the site (R_{Leaves}, $R_{Coarse\ roots}$, $NPP_{Coarse\ roots}$, NPP_{Stems} <10 cm dbh), but were estimated from measurements in similar Amazon forests, or taken from the literature. In recognition of the uncertainty entailed by this approach, we have assigned particularly wide error values to these estimates. A description of the overall approach and assumptions made in estimating components is presented in Tables 1 and 2.

Results

Climate

Solar radiation was high throughout the year and showed relatively moderate seasonal variation, with a minimum in the late wet season and a maximum in the mid-late dry season (Figure 2). Total annual radiation was among the highest found in the Amazon region. Mean monthly temperature varied between 24°C and 27°C, with the highest temperatures in the late dry season. Precipitation was highly seasonal, with an intense five-month dry season (May–September) with very little rain, countered by very high rainfall rates (>350 mm month^{-1}) at the peak of the wet season (December–January). Mean surface (0–30 cm) annual soil moisture content was not significantly different ($P < 0.001$) in the control plot (10.7 ± 0.20%) than in the burn plot (10.8 ± 0.2% water) (Figure 2). Wet season soil moisture values peaked at ca. 15%, and the dry season minimum was ca. 7%. The burn plot soils appeared to rehydrate more rapidly in the wet season. The mean MCWD was estimated to be –482 mm, towards the lower limit for tropical forest persistence (Malhi et al. 2009b)

Above-ground woody biomass and NPP

The mean height of canopy trees (≥40 cm dbh) was 24.9 ± 3.5 m for the control plot and 22.1 ± 2.4 m for the burn plot. Total above-ground biomass for trees ≥10 cm dbh was 75.2 Mg C ha^{-1} on the control and 57.8 Mg C ha^{-1} on the burn plot, indicating a substantial reduction

Table 1.   Methods for intensive monitoring of carbon dynamics on the control and annually burnt plots in Fazenda Tanguro, Mato Grosso state, Brazil (see also online supplemental material and RAINFOR-GEM manual 2012).

	Component	Method	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 were censused within the study area in each plot to determine the growth rate of existing surviving trees, mortality and recruitment. Growth of smaller trees was not directly measured, but a value was taken from a study in a similar forest in Bolivia (Araujo-Murakami et al. 2014).	2009–2011	Every year
		Seasonal growth: dendrometers were installed on ca. 65% of trees (≥ 10 cm dbh) in the plots to determine the spatial–temporal variation in growth.	2009–2011	Every three months
	Branch turnover net primary productivity ($NPP_{Branch\ turnover}$)	Branches (excluding those fallen from dead trees) were surveyed within a 1×400 m^2 transect in each plot; 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.	2009–2011	Every three months
	Litterfall net primary productivity ($NPP_{Litterfall}$)	Litterfall production of dead organic material ≥ 2 cm diameter was estimated by collecting litterfall in 25 litter traps 50 cm $\times$ 50 cm^2 in size placed 1 m above the ground at 20 m intervals within each plot.	2009–2011	Every 15 days
	Leaf area index (LAI)	LAI was recorded at 10 points per plot with an LAI–2000 sensor. Measurements were taken early in the morning or during overcast conditions to minimise direct sunlight.	2009–2011	Every month
	Loss to leaf herbivory ($NPP_{Herbivory}$)	Herbivory was not measured directly at the site, but a mean value was taken from a fertile site in south-eastern Peru and at infertile sites in eastern Brazil (Malhi et al. 2014; da Costa et al. 2014; Doughty et al. 2014) where leaves were collected in 25 litterfall traps and photographed prior to being dried.	n/a	Not directly measured
Below-ground net primary productivity (NPP_{BG})	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).	n/a	Not directly measured
	Fine root net primary productivity ($NPP_{Fine\ roots}$)	Sixteen in-growth cores (mesh cages 12 cm diameter) were installed to 30 cm depth at 30 m intervals in each plot. Cores were extracted and roots manually removed from the soil samples in four 10-min steps (Metcalfe et al. 2007b). Root-free soil was then re-inserted into the in-growth core. Collected roots were thoroughly rinsed, oven dried at 80 °C to constant mass, and weighed. This process was repeated for each measurement thereafter.	2009–2011	Every three months
Autotrophic and heterotrophic respiration	Total soil CO$_2$ efflux (R_{Soil})	Total soil CO$_2$ efflux was measured at 25 points every 20 m in each plot using a closed dynamic chamber method with an infra-red gas analyser (EGM-4) and soil respiration chamber (SRC–1) sealed to a permanent collar in the soil.	2009–2011	Every month
	Soil CO$_2$ efflux partitioned into autotrophic ($R_{Rhizosphere}$) and heterotrophic ($R_{Soilhet}$) components	At four points in each plot, we placed pairs of plastic tubes (12 cm diameter) with one surface tube in each pair permitting both $R_{Soilhet}$ and $R_{Rhizosphere}$, and the other tube in the pair inserted to 30 cm soil depth excluding $R_{Rhizosphere}$. At the centre of each study area, an additional set of tubes were installed to quantify and correct for the effect of soil disturbance during tube installation.	2009–2011	Every month
	Canopy respiration (R_{Leaves})	Canopy respiration was not directly measured at the site, instead we took a value for this term intermediate between a wetter, eastern Amazon site (da Costa et al. 2014) and a dry, western Amazon site (Araujo-Murakami et al. 2014).	n/a	Not directly measured
	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.	2009–2011	Every month
	Coarse root respiration ($R_{Coarse\ roots}$)	This component of respiration was not measured directly so was estimated by multiplying estimated above-ground live wood respiration by 0.21 ± 0.03, 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

Table 2. Data analysis techniques for intensive monitoring of carbon dynamics on the control and annually burnt plots in Fazenda Tanguro, Mato Grosso State, Brazil (see also online supplemental material and RAINFOR–GEM manual 2012).

Component		Data processing description
Above-ground net primary productivity (NPP_{AG})	Above-ground coarse wood net primary productivity (NPP_{ACW})	Biomass was calculated using the Chave et al. (2005) allometric equation for tropical 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 was 47.3% carbon (Martin and Thomas 2011). Tree height data were estimated by applying the allometric equation of Feldpausch et al. (2011).
	Branch turnover net primary productivity ($NPP_{Branch\ turnover}$)	See the RAINFOR-GEM manual (Version 2.2, 2012) for a description of decomposition status and surface area formulas. The manual is available for download at http://gem.tropicalforests.ox.ac.uk/
	Litterfall net primary productivity ($NPP_{Litterfall}$)	Litterfall was separated into foliar and non-foliar material, oven dried at 80°C to constant mass and weighed. Litter was estimated to contain 49.2% carbon, based on mean Amazonian values (Patiño et al. 2012).
	Leaf area index (LAI)	The LAI-2000 automatically calculates LAI with an algorithm using canopy gap fraction in different zenithal angles recorded through a fish-eye light sensor. LAI were partitioning 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 at 30° in this study.
	Loss to leaf herbivory ($NPP_{Herbivory}$)	Leaf area with and without holes were determined with image analysis software (ImageJ, NIH, USA). The fractional herbivory (H) for each leaf was then calculated as: $H = (A_{nh} - A_h) / A_{nh}$, 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. Total error was calculated as sample error plus 20% of the mean value.
Below-ground net primary productivity (NPP_{BG})	Coarse root net primary productivity ($NPP_{Coarse\ roots}$)	See RAINFOR-GEM manual (Version 2.2, 2012) for a description and range of root:shoot ratios. The manual is available for download at http://gem.tropicalforests.ox.ac.uk/. Total error was calculated as sample error plus 20% of the mean value.
	Fine root net primary productivity ($NPP_{Fine\ roots}$)	Roots were manually removed from the soil samples in four 10-minute time steps, to predict root extraction beyond 40 min (up to 100 min). This approach added on average 28% and 17% to initial estimates of root mass manually extracted from cores on the control and burn plots respectively. 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})	Respiration rates were calculated from the linear rate of increase in CO$_2$ concentration within the chamber (Metcalfe et al. 2007a). Curves were carefully checked for non-linearities and anomalies before use.
	Soil CO$_2$ efflux partitioned into autotrophic ($R_{Rhizosphere}$) and heterotrophic ($R_{Soilhet}$) components	Respiration rates were calculated from the linear rate of increase in CO$_2$ concentration within the chamber (Metcalfe et al. 2007a). Curves were carefully checked for non-linearities and anomalies before use. CO$_2$ efflux from the tubes inserted to 30 cm represents $R_{Soilhet}$, including some component of disturbance associated with tube installation. A separate experiment quantifying changes in CO$_2$ efflux associated with installation of deep tubes was used to correct $R_{Soilhet}$. The difference in CO$_2$ efflux between tubes inserted to 30 cm soil depth and only in the soil surface is taken as $R_{Rhizosphere}$.
	Canopy respiration (R_{Leaves})	To scale to canopy-level values, dark respiration for shade 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. (2009a) (67% of daytime leaf dark respiration, 34% of total leaf dark respiration). Total error was calculated as sample error plus 20% of the mean value.
	Above-ground live wood respiration (R_{Stems})	Respiration rates were calculated from the linear rate of increase in CO$_2$ concentration within the chamber (Metcalfe et al. 2007a). Curves were carefully checked for non-linearities and anomalies before use. To estimate plot-level stem CO$_2$ efflux per unit bole area was multiplied by bole surface area (SA) for each tree, estimated with the following equation (Chambers et al. 2004): $\log(SA) = -0.105 - 0.686 \log(dbh) + 2.208 \log(dbh)^2 - 0.627 \log(dbh)^3$, where H is tree height, and dbh is bole diameter at 1.3 m height. Finally, for each individual tree we regressed mean annual bole respiration against total annual growth. This relationship across all 25 trees for which we made R_{stem} measurements was then applied to the remaining community of trees in each plot, to estimate R_{stem} based upon their annual growth data.
	Coarse root respiration ($R_{Coarse\ roots}$)	Total error for this component was calculated as sample error plus 20% of the mean value.

of above-ground biomass resulting from the annual burning treatment. On the other hand, the mean NPP_{ACW} of trees ≥ 10 cm dbh was similar on the two plots, at 2.25 ± 0.23 Mg C ha^{-1} year^{-1} for the control plot and 2.19 ± 0.22 Mg C ha^{-1} year^{-1} for the burn plot. This implies that the fewer trees present on the burn plot maintained a higher rate of growth per tree than the control. Including trees ≤ 10 cm dbh ($17 \pm 6\%$ of total), we estimated a total NPP_{ACW} of 2.63 ± 0.29 and 2.56 ± 0.28 Mg C ha^{-1} year^{-1} for the control and burn plots, respectively (Table 3, Table 4, Figure 3, Figure 4). Dividing stem biomass by total NPP_{ACW}, we estimated a stem biomass residence time of ca. 29 years for the control plot.

Canopy NPP. LAI averaged 4.13 m^2 m^{-2} in the control plot and 2.53 m^2 m^{-2} in the burn plot, a significant difference ($P < 0.001$). There was surprisingly little seasonality in estimated LAI, despite the large seasonal cycle in litterfall. This suggests that there was turnover of leaves in the canopy, with the production of new leaves overlapping with the abscission of old leaves.

Mean annual LAI in the burn plot declined from 2.77 ± 0.19 m^2 m^{-2} in 2009 to 2.13 ± 0.16 m^2 m^{-2} in 2011. If we assume the specific leaf area to be 0.012 ± 0.003 g m^{-2} (intermediate between an infertile humid forest in the eastern Amazon and the more fertile deciduous forests in the western Amazon, Araujo-Murakami et al. 2014; da Costa et al. 2014), this is equivalent to a net canopy biomass loss rate of 0.27 ± 0.12 Mg C ha^{-1} year^{-1}. Hence our assumption of equilibrium in canopy biomass was not valid for the burn plot, since abscised leaves were clearly not entirely replaced by newly grown foliage. Therefore, $NPP_{Litterfall}$ on the burn plot was calculated as the litterfall rate minus the annual rate of loss of leaf biomass (Table 3, Table 4, Figure 3, Figure 4). In the control plot, there was no significant net change in *LAI* over the three years, and we therefore assume that litterfall gave a reasonable proxy for canopy production of fine organic matter.

Both sites showed a broad peak in canopy litterfall between May and October, closely tracking the seasonal pattern of radiation (Figure 5). $NPP_{Litterfall}$ was significantly greater ($P < 0.001$) at the control plot (5.00 ± 0.47 Mg C ha^{-1} year^{-1}) than at the burn plot (4.48 ± 0.48 Mg C ha^{-1} year^{-1}) (Table 3, Table 4, Figure 3, Figure 4).

$NPP_{Branch\ turnover}$ averaged 0.08 ± 0.01 Mg C ha^{-1} year^{-1} at the control plot but was very low (0.05 ± 0.01 Mg C ha^{-1} year^{-1}) at the burn plot. There was a strong seasonal cycle in the control plot, branch fall being greatest in the wet season and lowest in the dry season.

Below-ground NPP

$NPP_{Fine\ roots}$ was relatively low compared with other ecosystem components of NPP. We detected a significant effect of fire ($P < 0.001$) in the year of measurement, with fine root NPP of 1.86 ± 0.13 Mg C ha^{-1} year^{-1} in the control plot, compared with just 0.96 ± 0.05 Mg C ha^{-1} year^{-1} after the burn treatment (Table 3, Table 4, Figure 3, Figure 4). Both plots exhibited a strong seasonal cycle in $NPP_{Fine\ roots}$, declining during the dry season (Figure 5). Estimated $NPP_{Coarse\ roots}$ was ca. 0.5 Mg C ha^{-1} year^{-1} on both plots.

Table 3. Summary of carbon fluxes on the control and annually burnt plots over 2009–2011 in Fazenda Tanguro, Mato Grosso state, Brazil. Net primary productivity (NPP), gross primary productivity (GPP), plant carbon expenditure (PCE) and respiration components are in units of Mg C ha^{-1} year^{-1}. Carbon use efficiency (CUE) is calculated as total NPP / GPP or PCE. Sample error is uncertainty caused by spatial heterogeneity of the measured parameter within the study plots (standard error of the mean). Total error includes sample error together with an estimate of uncertainties due to measurement/equipment biases and up-scaling localised measurements to the plot level.

	Control plot			Burn plot		
	Mean	Sample error	Total error	Mean	Sample error	Total error
Net primary productivity						
Fine litter	5.00	0.47	0.47	4.48	0.48	0.48
Loss to herbivory	0.32	0.20	0.26	0.28	0.18	0.23
Branch turnover	0.08	0.01	0.01	0.05	0.01	0.01
Stems	2.63	0.25	0.29	2.56	0.24	0.28
Coarse roots	0.47	0.05	0.14	0.46	0.05	0.14
Fine roots	1.86	0.13	0.13	0.96	0.05	0.05
Respiration						
Leaves	7.48	0.80	2.30	5.29	0.50	1.55
Stems	4.57	0.45	1.82	5.29	0.18	1.77
Rhizosphere	3.30	0.30	0.63	4.00	0.49	0.89
Coarse roots	0.96	0.17	0.36	1.11	0.16	0.39
Soil heterotrophs	11.17	1.01	1.01	6.73	0.84	0.84
Ecosystem totals						
R_a	16.31	0.98	3.02	15.69	0.74	2.54
NPP	10.36	0.58	0.64	8.80	0.57	0.62
GPP / PCE	26.67	1.14	3.09	24.49	0.93	2.62
CUE	0.39	0.03	0.08	0.36	0.03	0.08

Table 4. Carbon allocation patterns on the control and annually burnt plots over 2009–2011 in Fazenda Tanguro, Mato Grosso state, Brazil. All values are percentages of total plant carbon expenditure (PCE), in components of net primary productivity (NPP) and autotrophic respiration (R_a). The stems NPP component includes contributions from branch turnover. Sample error is uncertainty caused by spatial heterogeneity of the measured parameter within the study plots (standard error of the mean). Total error includes sample error together with an estimate of uncertainties due to measurement/equipment biases and up-scaling localised measurements to the plot level.

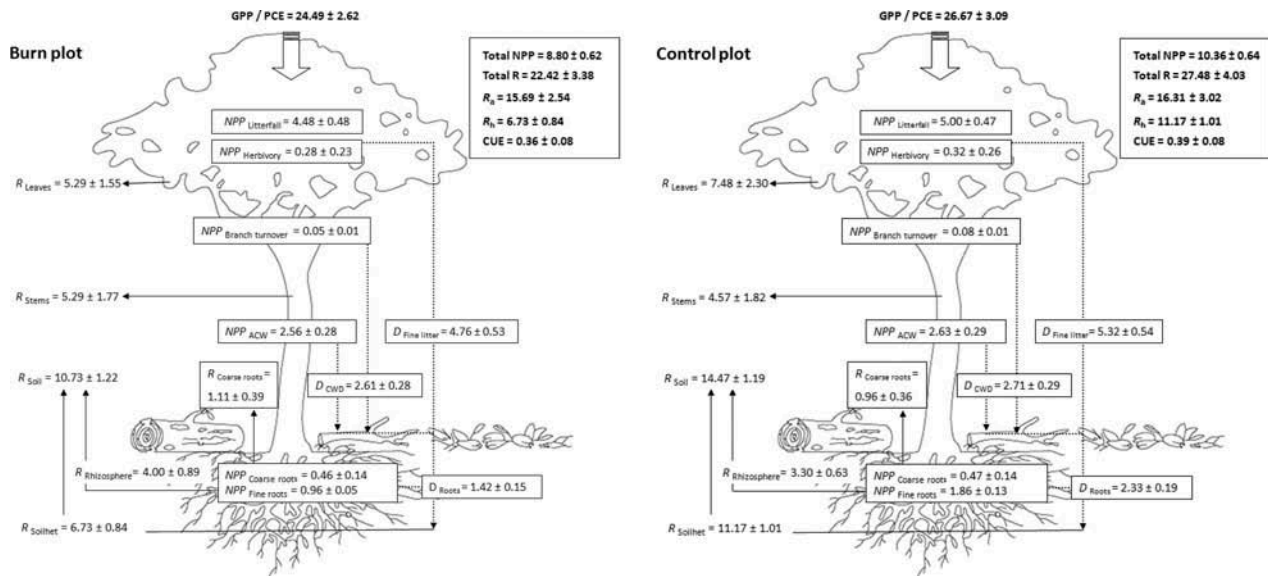|	Control plot			Burn plot		
	Mean	Sample error	Total error	Mean	Sample error	Total error
NPP						
Canopy	51	6	6	54	7	7
Stems	26	3	3	30	3	3
Roots	22	2	2	16	1	3
R_a						
Leaves	46	6	16	34	4	11
Stems	28	3	12	34	2	13
Roots	26	3	7	33	4	8
PCE (NPP + R_a)						
Canopy	48	4	10	41	3	8
Stems	27	2	8	32	2	8
Roots	25	2	4	27	2	5

Figure 3. Diagram showing the magnitude and pattern of key carbon fluxes on the control and annual burn plots in 2009–2011 in Fazenda Tanguro, Mato Grosso State, 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 Mg C ha^{-1} year^{-1}, with the exception of carbon use efficiency (CUE), which is calculated as total NPP/GPP or PCE. GPP = gross primary productivity, PCE = plant carbon expenditure, 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.

Soil CO₂ efflux

Total R_{soil}, incorporating both autotrophic ($R_{Rhizosphere}$) and heterotrophic ($R_{Soilhet}$) components, showed a significant seasonal cycle at both sites ($P < 0.001$), declining with soil moisture, and was lowest between May and September at both sites (Figure 6). Total annual R_{Soil} was significantly different between sites ($P < 0.001$), averaging 14.47 ± 1.19 Mg C ha^{-1} year^{-1} at the control plot and 10.73 ± 1.22 Mg C ha^{-1} year^{-1} at the burn plot (Table 3, Figure 3). $R_{Rhizosphere}$ exhibited a significant seasonal cycle

($P < 0.001$) that was similar in both sites and was lowest in the dry season (Figure 6). On an annual basis, $R_{Rhizosphere}$ was not significantly different between sites, averaging 3.30 ± 0.63 and 4.00 ± 0.89 Mg C ha^{-1} year^{-1} at the control and burn plots respectively (Table 3, Table 4, Figure 3, Figure 4). $R_{Soilhet}$ also showed a significant seasonal cycle ($P < 0.001$) in the control plot, and was lowest in the dry season (Figure 6). In the burn plot, the annual value of $R_{Soilhet}$ was lower and the seasonal cycle was weaker, in particular not rising to high values in the dry season as
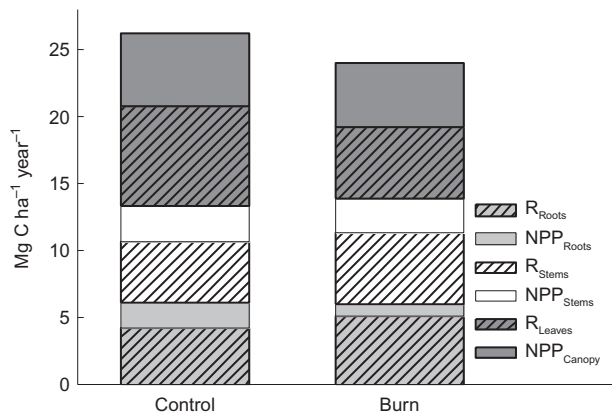
Figure 4.   Allocation of plant carbon to different components on the control and annual burn plots over 2009–2011 in Fazenda Tanguro, Mato Grosso State, Brazil. Components with prefixes R and NPP denote respiration and net primary productivity terms, respectively. Detailed descriptions of C flux components measured are presented in Tables 1 and 2. $NPP_{Canopy} = NPP_{Litterfall} + NPP_{Herbivory}$. $NPP_{Roots} = NPP_{Fine\ roots} + NPP_{Coarse\ roots}$. $NPP_{Stems} = NPP_{ACW} + NPP_{Branch\ turnover}$. $R_{Roots} = R_{Rhizosphere} + R_{Coarse\ roots}$.

observed on the control plot (Figure 6). Annual $R_{Soilhet}$ was significantly lower at the burn site ($P < 0.05$), averaging 6.73 ± 0.84, compared to 11.17 ± 1.01 Mg C ha^{-1} year^{-1} at the control plot (Table 3, Figure 3).

Live stem CO_2 efflux

CO_2 efflux per unit stem area was significantly lower ($P < 0.001$) on the control plot (0.91 ± 0.04 µmol m^{-2} s^{-1}) compared to a mean value of 1.25 ± 0.05 µmol m^{-2} s^{-1} for the burn plot (Figure 7). There was a significant positive linear relationship between NPP_{ACW} and R_{Stems} for both the control plot and the burn plot, although the R^2 for this relationship was below 0.05 for both plots. The best fit equation for the control plot was

$$R_{Stems} = 99 \times NPP_{ACW} + 0.47, \qquad (6)$$

and for the burn plot

$$R_{Stems} = 26 \times NPP_{ACW} + 0.64, \qquad (7)$$

where NPP_{ACW} and R_{Stems} are in units of Mg C ha^{-1} month^{-1} and µmol m^{-2} s^{-1}, respectively.

There was a significant seasonal cycle ($P < 0.001$) in R_{Stems} at both sites, related to the stem growth and precipitation cycle (Figure 7). When CO_2 efflux per unit stem area was up-scaled with plot-level stem area estimates, the resulting estimate of R_{Stems} was significantly greater ($P < 0.01$) at the burn plot (5.29 ± 1.77 Mg C ha^{-1} year^{-1}) than at the control plot (4.57 ± 1.82 Mg C ha^{-1} year^{-1}) (Table 3, Table 4, Figure 3, Figure 4).

Leaf respiration and photosynthesis

Based on the site *LAI* data and the mean of leaf respiration values found at other seasonal lowland Amazon forests

(Araujo-Murakami et al. 2014; da Costa et al. 2014), we estimated a total R_{Leaves} of 7.48 ± 2.30 Mg C ha^{-1} year^{-1} in the control plot and 5.29 ± 1.55 Mg C ha^{-1} year^{-1} in the burn plot (Table 3, Table 4, Figure 3, Figure 4). The difference between the two plots was due entirely to the difference in *LAI*.

Total NPP, GPP and CUE

The individual component*s* of NPP were summed to give an estimate of total NPP of 10.36 ± 0.64 Mg C ha^{-1} year^{-1} for the control plot and 8.80 ± 0.62 Mg C ha^{-1} year^{-1} for the burn plot. Similarly, the components of R_a were summed to give an estimate of total R_a as 16.31 ± 3.02 and 15.69 ± 2.54 Mg C ha^{-1} year^{-1} for the control and burn plots, respectively. The sum of NPP and R_a yielded an estimated PCE of 26.67 ± 3.09 Mg C ha^{-1} year^{-1} for the control plot and 24.49 ± 2.62 for the burn plot (Table 3, Table 4, Figure 3, Figure 4). The ratio of NPP to PCE gave an estimated CUE of 0.39 ± 0.08 at the control plot and 0.36 ± 0.08 at the burn plot.

Discussion

Broad similarities in carbon cycling across plots highlighting forest fire tolerance

Despite the severity of the fire treatment at the study site, we found quite subtle shifts in C cycling on the burn plot relative to the control (Table 3, Table 4, Figure 3, Figure 8). Overall estimated NPP was reduced by 15%, while the estimated R_a was 4% lower on the burn plot relative to the control (Figure 8). In the case of NPP, all individual components declined, though $NPP_{Fine\ roots}$ and $NPP_{Litterfall}$ accounted for 91% of the overall reduction (Figure 8).

By contrast, the apparent lack of plot difference in R_a masked opposing responses from the individual components. For example, both $R_{Rhizosphere}$ and R_{Stems} actually increased on the burn plot, but this was largely offset by a substantial estimated decline in R_{Leaves} (Figure 8). This conclusion remains tentative, however, as leaf-level respiration rates were not directly measured on the two plots, instead a single site value was derived from other lowland forests. Hence, the large estimated decline in R_{Leaves} on the burn plot was entirely driven by the lower LAI on the plot compared to the control. Clearly, leaf-level physiology and gas exchange measurements at the site are a key priority in future studies to resolve the forest C balance at Tanguro.

We found significantly higher R_{Stems} on the burn plot compared to the control (Figure 7), yet plot-level NPP_{ACW} was similar (Table 3, Table 4, Figure 3, Figure 4). We hypothesise that this may reflect elevated maintenance respiration in the wood tissue on the burn plot, possibly due to damage repair costs incurred by the fire treatment. Similarly, despite a 48% decrease in $NPP_{Fine\ roots}$, probably caused by fire-associated destruction of surface root mats on the burn plot, $R_{Rhizosphere}$ actually increased by 21% relative to the control (Figure 8). This suggests either that
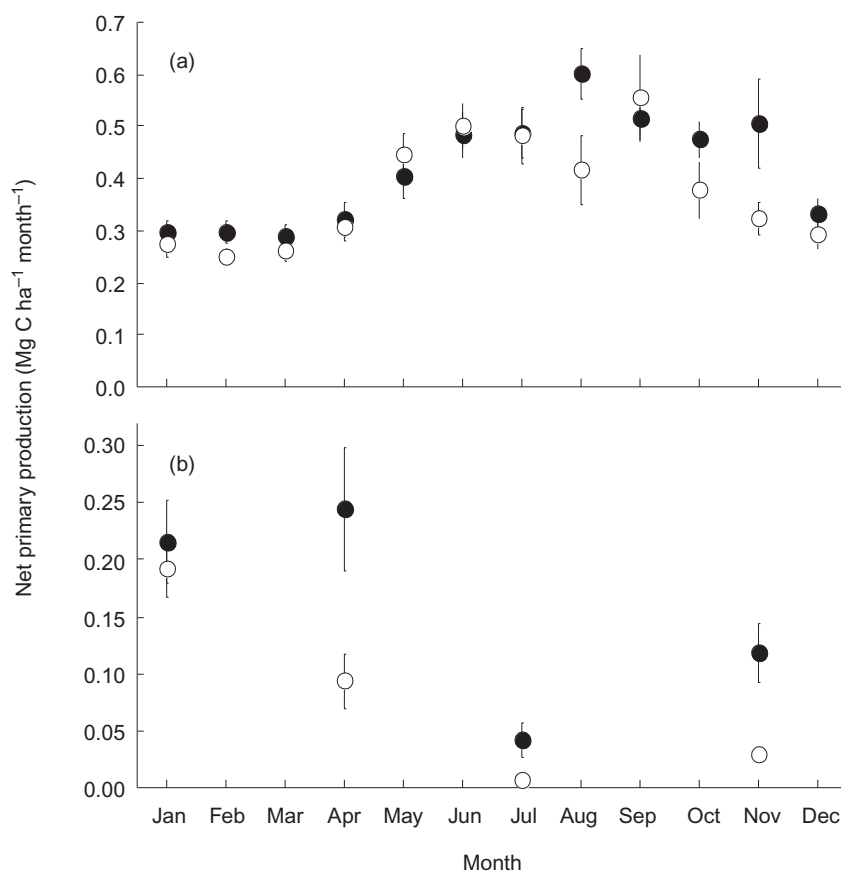
Figure 5.   Seasonal net primary production from (a) canopy fine litter and (b) fine roots on the control (filled circles) and annual burn plots (open circles) over 2009–2011 on the Fazenda Tanguro, Mato Grosso State, Brazil. Error bars are standard errors ($n = 16$ for roots and 10 for canopy fine litter).

root-specific respiration rates were elevated or that allocation to other rhizosphere components (mycorrhizae and exudate-dependent soil microbes) was substantially higher on the burn plot than the control. As an independent check on the accuracy of the soil respiration partitioning in this study we compared directly measured $R_{Soilhet}$ and soil C inputs from all of the *NPP* terms on the control plot. Under steady-state conditions, these two terms should approximately match one another (Raich and Nadelhoffer 1989), and on the control plot the measured $R_{Soilhet}$ diverged by 8% from the expected flux based on soil C input. Under the same steady-state assumptions, the difference between soil C input and R_{soil} should be approximately equivalent to total below-ground allocation (TBCA) to roots. Comparing this difference with the sum of $R_{Rhizosphere}$ and $NPP_{Fine\ roots}$ on the control plot, we again found reasonable agreement (26% divergence of the measured from the expected TBCA, equivalent to 1.1 Mg C ha^{-1} year^{-1}), which confirms that our approach successfully captured the broad pattern of soil CO_2 partitioning at the site.

There was strong seasonality in $R_{Rhizosphere}$, tracking seasonality in $NPP_{Fine\ roots}$, with the lowest values in the mid-late dry season (Figure 6). $R_{Soilhet}$ also showed a clear seasonal cycle, with a minimum in the mid-dry season (Figure 6). In the control plot $R_{Soilhet}$ started to rise in the late dry season (Figure 6), possibly as a consequence of

both increased litter inputs and rising rainfall (Figure 2, Figure 5). In the burn plot, the wet season rise in $R_{Soilhet}$ was muted (Figure 6). A probable reason for this was that much of the litter layer was combusted in the annual burn in September (and litterfall inputs were also lower), which probably resulted in diminished stocks of surface litter and labile soil organic matter.

The net consequence of these shifts in NPP and R_a was that the plots exhibited surprisingly similar estimated GPP/PCE values (Table 3, Figure 3), given the large reduction in both tree density and LAI on the burn plot. We note that as the burn plot degrades over time, our plant-level steady-state assumption may not be valid if vegetation was depleting non-structural carbohydrate reserves, and therefore that the PCE we recorded with our approach may have been be greater than C uptake via GPP. Expenditure of stored reserves of non-structural carbohydrates could account for higher plant PCE than GPP over limited periods of time. Alternatively, despite all efforts to minimise errors, some portion of R_a recorded in the present study may actually be heterotrophic in source. For example, a proportion of R_{Stems} may be derived from CO_2 generated by soil microbes and subsequently taken up in xylem solution (Levy et al. 1999; Teskey and McGuire 2002), though the general agreement between expected (from soil C inputs) and recorded $R_{Soilhet}$ indicated that this was not a major
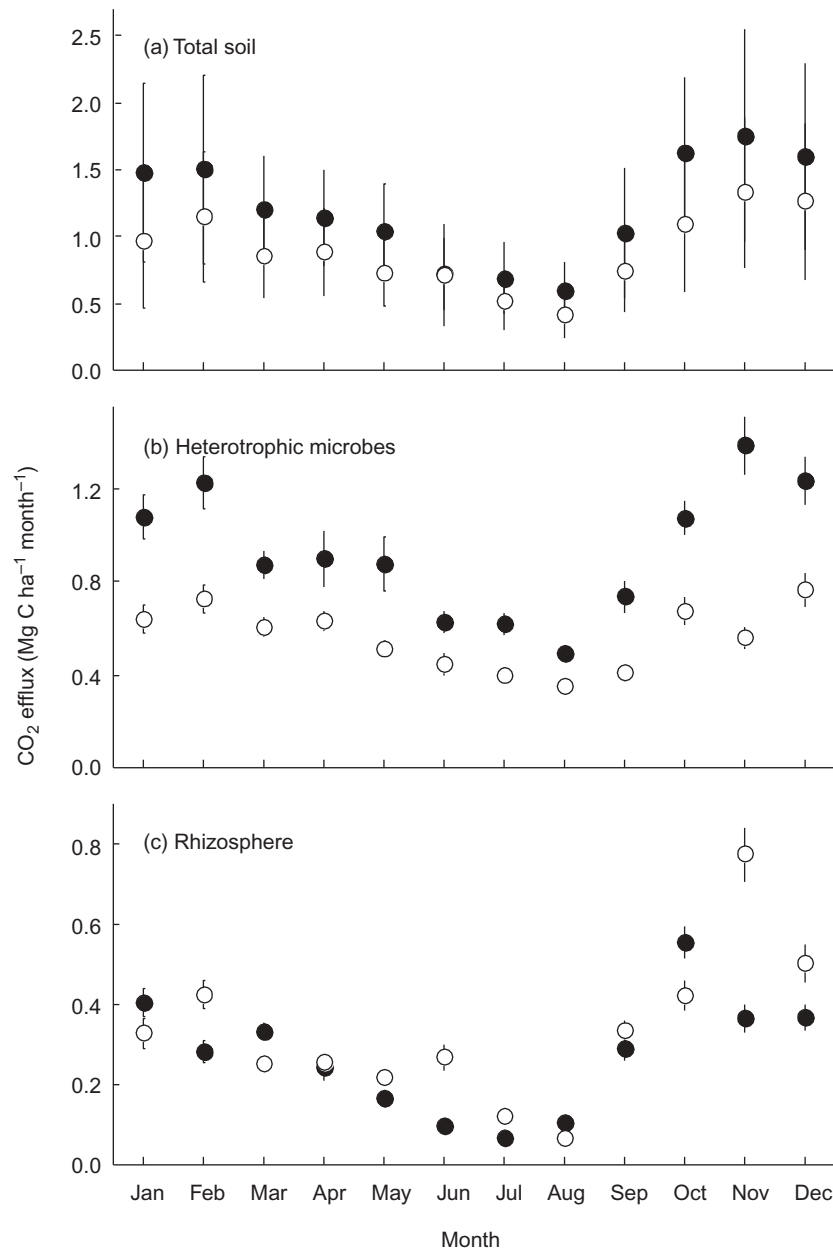
Figure 6.   Seasonality of total soil CO_2 efflux (a) and contributions to this total from heterotrophic soil microbes (b) and rhizospheric sources (c) on the control (filled circles) and annual burn plots (open circles) over 2009–2011 in Fazenda Tanguro, Mato Grosso State, Brazil. These estimates do not include the contribution of coarse roots. Error bars are standard errors.

problem at the site. In addition, the similar CUE estimated for both sites suggested that R_a for the burn plot was not disproportionately high compared to NPP.

Distinctive patterns of carbon use at the dry southern Amazon forest ecotone

The high value of CUE at both the control and burn plots is noteworthy (Table 3, Figure 3). CUE values of ca. 0.30 have previously been reported from undisturbed sites in the humid forest zone of the Brazilian Amazon (Malhi 2012). As there was no evidence of recent disturbance in the control plot, the high CUE values appear to be a consequence of the high natural dynamism of this site, with stem turnover rates of 3% on the control plot (Balch et al. 2011) compared to ≤2% in most humid Amazonian forests. This results in a relatively short estimated woody biomass residence time of ca. 29 years for the control plot, compared to typical residence times for Amazonian forests of between 50 and 100 years. This conclusion requires further testing and validation at other similar sites to assess whether these properties are a general facet of these ecotonal forests, or whether the study site is anomalous in this respect. However, a study from forests in Kenia, Bolivia, which have a comparable rainfall regime but more fertile soils, has reported similar woody biomass residence times
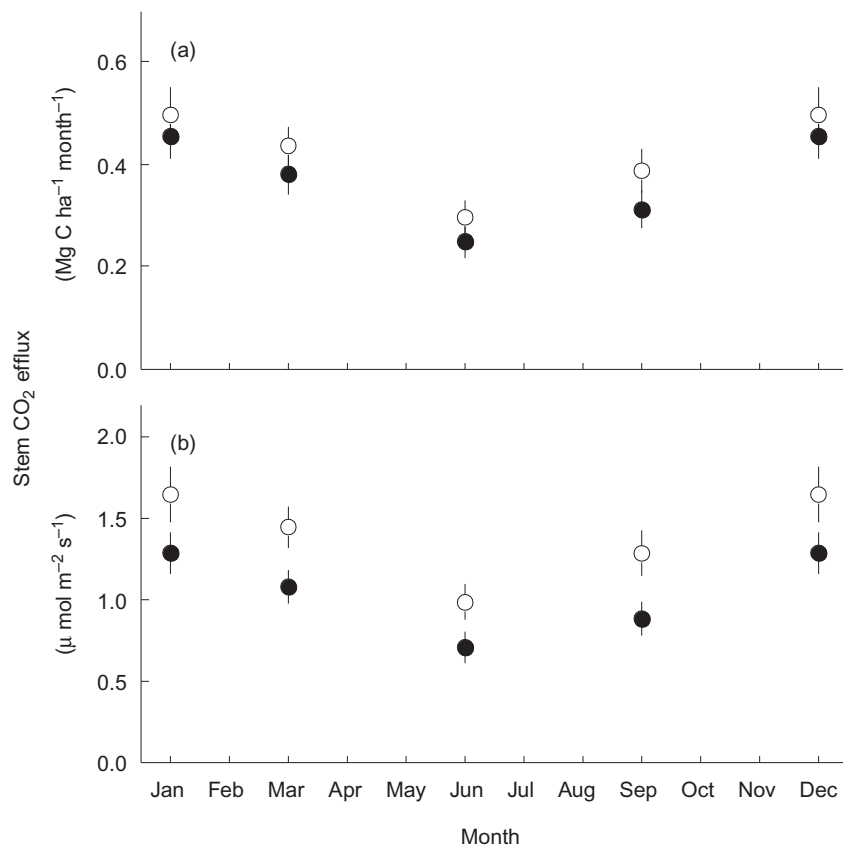
Figure 7. Seasonality of stem CO_2 efflux on (a) a stand-level and (b) a stem area basis on the control (filled circles) and annual burn plots (open circles) over 2009–2011 in Fazenda Tanguro, Mato Grosso State, Brazil. Error bars are standard errors (*n* for 7(b) = 25).
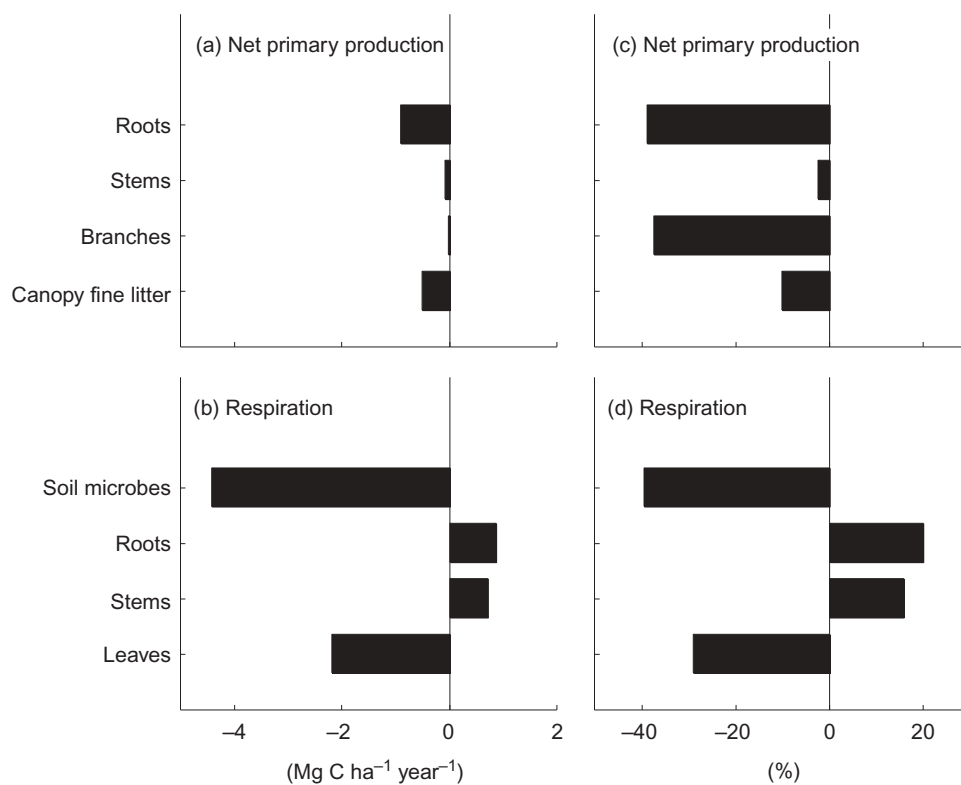

Figure 8. Absolute (a, b) and relative differences (c, d) in ecosystem carbon allocation to different components on the control and annual burn plots over 2009–2011 in Fazenda Tanguro, Mato Grosso State, Brazil.

of 22–26 years and CUE of ca. 0.40 (Araujo-Murakami et al. 2014). Taken together, these studies provide the first evidence that the humid Amazon forest biome is fringed by a distinctive peripheral forest zone characterised by highly dynamic forests with relatively high CUE. Thus, despite potentially lower rates of GPP in the drought-adapted forest at this study site, rates of biomass production were not greatly different from those in the more humid Amazonian forests.

Conclusions

This paper presents the first comprehensive quantification of the C cycle of unburnt and annually burnt transition forest plots in Amazonia. The most noteworthy feature is the similarity in respiration, biomass production and allocation between the two plots, regardless of the annual burn in one plot. This suggests that many aspects of productivity and C cycling in these transitional forests are not greatly affected by frequent, low intensity understorey fires. In addition, our measurements indicate that this forest consists of shorter-lived trees with a higher CUE compared to trees in wetter, lowland forests in the interior of Amazonia.

The study has demonstrated the potential of a comprehensive, multiple-component approach to quantifying and understanding the mechanisms controlling the C cycle in tropical forests.

Acknowledgements

Notes on contributors

Wanderley Rocha is a research assistant. He is currently undertaking a research as part of a Masters degree, with emphasis on soil ecology.

Daniel B. Metcalfe is an Associate Professor. His research focuses broadly on the impact of climate change on terrestrial carbon cycling.

Chris E. Doughty is an earth system scientist and studies the interaction between tropical forests and climate.

Paulo Brando's research explores the effects of climate change and land use on the impoverishment of the Amazon forests through the use of ecological experiments, dynamic vegetation and statistical models, and remote sensing techniques.

Divino Vicente Silvério is a doctoral student in ecology and his research focus is the carbon and energy balance in the Amazon.

Kate Halladay is a post-doctoral researcher, specialising in meteorology, particularly in tropical systems.

Daniel C. Nepstad is director of the International and Amazon Scenarios. His ecological research ranges between the response of Amazon forests to climate change and fire, and integrated assessments of policy scenarios. His policy analysis focuses on tropical deforestation, low-emission development and commodity market transformation.

Jennifer K. Balch is an assistant professor. She is an earth systems ecologist, with an interest in the patterns and processes underlying fire disturbance and ecosystem recovery, particularly in tropical forests.

Yadvinder Malhi is a Professor of Ecosystem Science. His research interests include the functioning and ecophysiology of tropical forest ecosystems in the context of global atmospheric change. He coordinates a network of forest research sites across the tropics.

References

Alencar A, Nepstad D, McGrath D, Moutinho P. 2004. Desmatamento na Amazônia: indo além da "emergência crônica". Belém (Brazil): IPAM.

Alencar A, Nepstad D, Moutinho P. 2005. Carbon emissions associated with forest fires in Brazil. In: Moutinho P, Schwartzman S, editors. Tropical deforestation and climate change. Belém (Brazil): IPAM. p. 23–33.

Alencar A, Nepstad DC, Vera Diaz MC. 2006. Forest understory fire in the Brazilian Amazon in ENSO and non-ENSO Years: Area burned and committed carbon emissions. Earth Interactions 10:1–17.

Aragão LEOC, Malhi Y, Roman-Cuesta RM, Saatchi S, Anderson LO, Shimabukuro YE. 2007. Spatial patterns and fire response of recent Amazonian droughts. Geophysical Research Letters 34:L07701. doi:10.1029/2006GL028946.

Aragão LEOC, Shimabukuro YE. 2010. The incidence of fire in Amazonian forests with implications for REDD. Science 328:1275–1278.

Araujo-Murakami A, Doughty CE, Metcalfe DB, Silva-Espejo JE, Arroyo L, Heredia JP, Flores M, Sibler R, Mendizabal LM, Pardo-Toledo, et al. 2014. The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia. Plant Ecology and Diversity 7(1–2):55–69.

Balch JK, Nepstad DC, Brando PM, Curran LM, Portela O, de Carvalho O, Lefebvre P. 2008. Negative fire feedback in a transitional forest of southeastern Amazonia. Global Change Biology 14:2276–2287.

Balch JK, Nepstad DC, Curran LM, Brando PM, Portela O, Guilherme P, Reuning-Scherer JD, de Carvalho Jr O. 2011. Size, species, and fire behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon. Forest Ecology and Management 261:68–77.

Behling H, Bauermann SG, Neves PCP. 2001. Holocene environmental changes in the São Francisco de Paula region, southern Brazil. Journal of South American Earth Sciences 14:631–639.

Brando PM, Nepstad DC, Balch JK, Bolker B, Christman MC, Coe M, Putz FE. 2012. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density, and fire behavior. Global Change Biology 18: 630–641.

Bush MB, de Oliveira PE, Miller MC, Moreno E, Colinvaux PA. 2004. Amazonian paleoecological histories: one hill, three watersheds. Palaeogeography, Palaeoclimatology, Palaeoecology 214:359–393.

Cairns MA, Brown S, Helme EH, Baumgardner GA. 1997. Root biomass allocation in the world's upland forests. Oecologia 111:1–11.

Cardoso MF, Hurtt GC, Moore B, Nobre CA, Prins EM. 2003. Projecting future fire activity in Amazonia. Global Change Biology 9:656–669.

Carpenter SR. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:677–680.

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.

Chapin FS, Woodwell GM, Randerson JT, Lovett GM, Rastetter EB, Baldocchi DD, Lark DA, Harmon ME, Schimel DS, Valentini R, et al. 2006. Reconciling carbon-cycle concepts, terminology, and methodology. Ecosystems 9:1041–1050.

Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster 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.

Cochrane MA. 2001. Synergistic interactions between habitat fragmentation and fire in evergreen tropical forests. Conservation Biology 15:1515–1521.

Cochrane MA, Alencar A, Schulze MD, Souza CM Jr, Nepstad DC, Lefebvre P, Davidson EA. 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. Science 284:1832–1835.

Cochrane MA, Laurance WF. 2008. Synergisms among fire, land use, and climate change in the Amazon. Ambio 37:522–527.

Cochrane MA, Schulze MD. 1999. Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition. Biotropica 31:2–16.

da Costa ACL, Metcalfe DB, Doughty CE, de Oliveira AAR, Neto GFC, da Costa MC, de Athaydes Silva Junior J, Aragão LEOC, Almeida S, Galbraith DR, et al. 2014. Ecosystem respiration and net primary productivity after 8–10 years of experimental through-fall reduction in an eastern Amazon forest. Plant Ecology and Diversity 7(1–2):7–24.

DeLucia EH, Drake JE, Thomas RB, Gonzalez-Meler M. 2007. Forest carbon use efficiency: is respiration a constant fraction of gross primary production? Global Change Biology 13:1157–1167.

Doughty CE, Goulden ML. 2008. Seasonal patterns of tropical forest leaf area index and CO_2 exchange. Journal of Geophysical Research – Biogeosciences 113:G00B06. doi: 10.1029/2007JG000590.

Doughty CE, Metcalfe DB, da Costa MC, de Oliveira AAR, Neto GFC, Silva JA, Aragão LEOC, Almeida SS, Quesada CA, Girardin CAJ, et al. 2014. 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 and Diversity 7(1–2):41–53.

Feldpausch TR, Banin L, Phillips OL, Baker TR, Lewis SL, Quesada CA, Affum-Baffoe K, Arets EJMM, Berry NJ, Bird M, et al. 2011. Height–diameter allometry of tropical forest trees. Biogeosciences 8:1081–1106.

Hammond DS, ter Steege H. 1998. Propensity for fire in the Guianan rainforests. Conservation Biology 12:944–947.

Haugaasen T, Barlow J, Peres CA. 2003. Surface wildfires in central Amazonia: short-term impact on forest structure and carbon loss. Forest Ecology and Management 179:321–331.

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.

Kauffman JB, Cumming DL, Ward DE. 1998. Fire in the Brazilian Amazon: 2. Biomass, nutrient pools and losses in cattle pastures. Oecologia 113:415–427.

Laurance WF, Williamson GB. 2001. Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. Conservation Biology 15:1529–1535.

Levy PE, Meir P, Allen SJ, Jarvis PG. 1999. The effect of aqueous transport of CO_2 in xylem sap on gas exchange in woody plants. Tree Physiology 19:53–59.

Malhi Y. 2012. The productivity, metabolism and carbon cycle of tropical forest vegetation. Journal of Ecology 100: 65–75.

Malhi Y, Amézquita FF, Doughty CE, Silva-Espejo JE, Girardin CAJ, Metcalfe DB, Aragão LEOC, Huaraca-Quispe LP, Alzamora-Taype I, Eguiluz-Mora L, et al. 2014. The productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western Amazonia, Peru. Plant Ecology and Diversity 7(1–2):85–105.

Malhi Y, Aragão LEOC, Galbraith D, Huntingford C, Fisher R, Zelazowski P, Sitch S, McSweeney C, Meir P. 2009a. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. Proceedings of the National Academy of Sciences, USA 106: 20610–20615.

Malhi Y, Aragão LEOC, Metcalfe DB, Paiva R, Quesada CA, Almeida S, Anderson L, Brando P, Chambers JQ, da Costa ACL. 2009b. Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. Global Change Biology 15:1255–1274.

Malhi Y, Grace J. 2000. Tropical forests and carbon dioxide. Trends in Ecology and Evolution 15:332–337.

Martin AR, Thomas SC. 2011. A reassessment of carbon content in tropical trees. PLoS ONE 6(8): e23533. doi:10.1371/journal.pone.0023533

Melillo JM, Houghton RA, Kicklighter DW, McGuire AD. 1996. Tropical deforestation and the global carbon budget. Annual Review of Energy and the Environment 21:293–310.

Metcalfe DB, Meir P, Aragão LEOC, Malhi Y, da Costa ACL, Braga A, Gonçalves PHL, de Athaydes J, de Almeida SS, Williams M. 2007a. 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:G04001. doi: 10.1029/2007JG000443.

Metcalfe DB, Meir P, Aragão LEOC, Lobo-do-Vale R, Galbraith D, Fisher RA, Chaves MM, Maroco JP, da Costa ACL, de Almeida SS, et al. 2010. Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon. New Phytologist 187:608–621.

Metcalfe DB, Williams M, Aragão LEOC, Da Costa ACL, De Almeida SS, Braga AP, Gonçalves PHL, De Athaydes Silva J Jr, Malhi Y, Meir P. 2007b. A method for extracting plant roots from soil which facilitates rapid samples processing without compromising measurement accuracy. New Phytologist 174:697–703.

Nepstad D, Carvalho G, Barros AC, Alencar A, Capobianco JP, Bishop J, Mountinho P, Lefebvre P, Lopes Silva U, Prins E. 2001. Road paving, fire regime feedbacks, and the future of Amazon forests. Forest Ecology and Management 154:395–407.

Nepstad D, Lefebvre P, Lopes da Silva U, Tomasella J, Schlesinger P, Solórzano L, Moutinho P, Ray D, Guerreira Benito J. 2004. Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. Global Change Biology 10:704–717.

Nepstad DC, Verissimo A, Alencar A, Nobre C, Lima E, Lefebvre P, Schlesinger P, Potter C, Moutinho P, Mendoza E, et al. 1999. Large-scale impoverishment of Amazonian forests by logging and fire. Nature 398:505–508.

Patiño S, Fyllas NM, Baker TR, Paiva R, Quesada CA, Santos AJB, Schwarz M, ter Steege H, Phillips OL, Lloyd J. 2012. Coordination of physiological and structural traits in Amazon forest trees, Biogeosciences 9:775–801

Quesada CA, Lloyd J, Schwarz M, Patiño 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.

Osmond B, Ananyev G, Berry J, Langdon C, Kolber Z, Lin G, Monson R, Nichol C, Rascher U, Schurr U, Smith S, Yakir D. 2004. Changing the way we think about global change research: scaling up in experimental ecosystem science. Global Change Biology 10:393–407.

Potter C, Klooster S and Genovese V. 2009. Carbon emissions from deforestation in the Brazilian Amazon region. Biogeosciences 6:2369–2381.

RADAM Brasil. 1974. Folha SA 22. Rio de Janeiro: DNP/MME. Projeto RADAM Brasil. Vol. 5, p. 478.

Raich JW, Nadelhoffer KJ. 1989. Below-ground carbon allocation in forest ecosystems global trends. Ecology 70: 1346–1354.

Silveira JAG, Araújo SAM, Lima JPMS, Viégas RA. 2009. Roots and leaves display contrasting osmotic adjustment mechanisms in response to NaCl-salinity in *Atriplex nummularia*. Environmental and Experimental Botany 66:1–8.

Stokstad E. 2005. Experimental drought predicts grim future for rainforest. Science 308:346–347.

Sullivan TJ. 1997. Ecosystem manipulation experimentation as a means of testing a biogeochemical model. Environmental Management 21:15–21.

Taylor JR. 1997. An introduction to error analysis: the study of uncertainties in physical measurements. Sausalito (USA): University Science Books.

Teskey RO, McGuire MA. 2002. Carbon dioxide transport in xylem causes overestimation of rates of respiration in trees. Plant, Cell and Environment 25:1571–1577.

Turcq B, Sifeddine A, Martin L, Absy ML, Volkmer-Ribeiro C. 1998. Amazonia rainforest fires: A lacustrine record of 7000 years. Ambio 27:139–142.

van der Werf GR, Randerson JT, Collatz GJ, Giglio L. 2003. Carbon emissions from fires in tropical and subtropical ecosystems. Global Change Biology 9:547–562.

Veloso HP, Rangel Filho ALR, Lima JCA. 1991. *Classificacão da vegetacão Brasileira adaptada a um sistema universal*. Rio de Janeiro (Brazil): IBGE.

Zelazowski P, Malhi Y, Huntingford C, Sitch S, Fisher JB. 2011. Changes in the potential distributions of humid tropical forests on a warmer planet. Philosophical Transactions of the Royal Society of London – Biological Sciences 369:137–160.