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Ecosystem respiration and net primary productivity after 8–10 years of experimental through-fall reduction in an eastern Amazon forest

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Background: There is much interest in how the Amazon rainforest may respond to future rainfall reduction. However, there are relatively few ecosystem-scale studies to inform this debate.

Aims: We described the carbon cycle in a 1 ha rainforest plot subjected to 8–10 consecutive years of ca. 50% through-fall reduction (TFR) and compare these results with those from a nearby, unmodified control plot in eastern Amazonia.

Methods: We quantified the components of net primary productivity (*NPP*), autotrophic (R_a) and heterotrophic respiration, and estimate gross primary productivity (*GPP*, the sum of *NPP* and R_a) and carbon-use efficiency (*CUE*, the ratio of *NPP*/*GPP*).

Results: The TFR forest exhibited slightly lower *NPP* but slightly higher R_a , such that forest *CUE* was 0.29 ± 0.04 on the control plot but 0.25 ± 0.03 on the TFR plot. Compared with four years earlier, TFR plot leaf area index and small tree growth recovered and soil heterotrophic respiration had risen.

Conclusions: This analysis tested and extended the key findings of a similar analysis 4 years earlier in the TFR treatment. The results indicated that, while the forest recovered from extended drought in some respects, it maintained higher overall R_a relative to the undroughted control, potentially causing the droughted forest to act as a net source of CO₂.

Keywords: drought; carbon cycling; Caxiuanã National Forest Reserve; climate change; tropical rainforest; biomass allocation; *CUE*; *GPP*; *NPP*; *PCE*

Introduction

The Amazon forest regulates the flow of large quantities of carbon dioxide and water into the atmosphere, thereby playing a major role in both regional and global climate (Field et al. 1998; Gedney and Valdes 2000; Malhi et al. 2002; Werth and Avissar 2002). At the same time, the region is rapidly changing in ways that could fundamentally alter the structure and function of the ecosystem, with potentially far-reaching consequences (Davidson et al. 2012). One important agent of change is an increase in the frequency and severity of drought associated with regional deforestation, fire and, not least, climate change, which is projected by a number of models (Werth and Avissar 2002; Christensen et al. 2007; Cox et al. 2008; Harris et al. 2008; Li et al. 2008; Malhi et al. 2009a; Spracklen et al. 2012). Although there remains substantial variation amongst models in terms of predicted future drought frequency and severity (Li et al. 2006; Jupp et al. 2010), some recent model analyses predict major potential shifts in Amazon C storage driven, in part, by moisture availability (e.g. Rammig et al. 2010), although the region appears less sensitive to warming than previously thought (Cox et al.

2013). Strong El Niño events, such as those in 1997 and 1998, have been associated with enhanced drought in eastern Amazonia (Christensen et al. 2007). Two unusually severe drought episodes, in 2005 and 2010, were linked to temporarily elevated Atlantic sea surface temperatures (Marengo et al. 2008, 2011; Zeng et al. 2008; Lewis et al. 2011). If a warmer Atlantic becomes a semi-permanent feature around the South American coast as global temperatures increase (Rayner et al. 2006), these types of extreme droughts could become more frequent and longer-lasting (Cox et al. 2008).

Several studies have provided key insights into the ecosystem impacts of these severe short-term droughts (e.g. Condit et al. 1995; Williamson et al. 2000; Asner et al. 2004; Nepstad et al. 2004; Phillips et al. 2009, 2010). However, it is unclear whether the results from these efforts also apply to forests facing severe, long-term drought. Hence, our understanding of the vulnerability of the Amazon forest to future climate change has been limited by the lack of field data to test model assumptions and outputs (Meir and Woodward 2010). In this context, two large-scale (each covering 1 ha) through-fall reduction

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(TFR) experiments in the Amazon have provided a crucial means of testing modelled representations of Amazon forest structure and function under soil moisture deficit (Nepstad et al. 2002, 2007; Davidson et al. 2004, 2008; Fisher et al. 2006, 2007; Metcalfe et al. 2007a, 2008, 2010a, 2010b; Sotta et al. 2007; Brando et al. 2008; Meir et al. 2008, 2009; da Silva et al. 2009; da Costa et al. 2010). While these experiments do not reproduce all the meteorological impacts of a drought (e.g. air temperature and humidity, rainfall seasonality), they provide key process-level data to constrain modelled responses of vegetation to one key drought component – an increase in soil moisture deficit. In some key respects, the forests seem relatively tolerant to a few consecutive years of soil moisture deficit, but after this initial period some threshold appears to be exceeded and a substantial increase in tree mortality rate follows, particularly amongst large individuals (Nepstad et al. 2007; da Costa et al. 2010). In addition to this most visible change in forest structure caused by mortality, the surviving forests show a range of shifts in growth, respiration and C allocation, which together alter their ability to sequester CO₂ from the atmosphere (e.g. Fisher et al. 2007; Brando et al. 2008; Meir et al. 2008; Metcalfe et al. 2010b).

Metcalfe et al. (2010b) provided a comprehensive summary of the C budget at one Amazon TFR experiment – in the Caxiuanã National Forest Reserve in eastern Amazonia, Brazil. This analysis used a mixture of data collected 4 years after commencement of the TFR treatment, data collected earlier from the same experiment and literature values to calculate annualised estimates of key ecosystem C fluxes. The analysis by Metcalfe et al. (2010b) documented several unusual patterns which merited further research. First, the authors reported a large drought-induced increase in plant respiration, despite evidence that soil moisture deficit usually inhibits respiration in actively growing plant tissues (Atkin and Macherel 2009, and references therein). Second, despite evidence that plants generally allocate more C below ground under moisture-limiting conditions (Litton et al. 2007), following long-established theory (Thornley 1972; Cannell and Dewar 1994) that underlies many current forest growth models (Lacointe 2000), Metcalfe et al. (2010b) found no clear increase in below-ground C allocation even after ca. 5 years of severe drought. The experiment is now the only ongoing large-scale TFR experiment in the Amazon and the longest-running experiment of its kind in the tropics.

In this study we measured the same components of ecosystem C cycling quantified by Metcalfe et al. (2010b), but after eight consecutive years of the TFR treatment and using a more extensive and more frequent suite of ecosystem C flux measurements. The overall objectives of this re-assessment were to (1) to examine the preliminary conclusions of the earlier analysis against more extensive and detailed dataset collected over a longer period of time; (2) to identify longer-term drought responses beyond the initial, transitional impacts of the first few drought years; and (3) to quantify drought impacts on the seasonality of ecosystem

C cycling. Specifically, we asked how the TFR treatment altered:

- (i) forest net primary productivity (*NPP*) and respiration from heterotrophic and autotrophic sources (R_a);
- (ii) allocation of *NPP* and R_a amongst leaves, stem and roots;
- (iii) total plant carbon expenditure ($PCE = NPP + R_a$) and carbon-use efficiency ($CUE = NPP/PCE$); and the
- (iv) magnitude and timing of seasonal variation in all components.

Materials and methods

Site characteristics

The experimental site is located in Caxiuanã National Forest Reserve, Pará in the eastern Brazilian Amazon (1°43'S, 51°27'W). It is a largely undisturbed *terra firme* forest (Lisboa and Ferraz 1999; Carswell et al. 2002), of the type widespread across eastern Amazonia (Quesada et al. 2012). The study plots are located on highly weathered Vetic Acrisols typical of upland forests in the eastern Amazon, with a thick stony laterite layer at 3–4 m depth (Quesada et al. 2010). The site elevation is 15 m above river level in the dry season and the water table has been occasionally observed at a soil depth of 10 m during the wet season. The site has a climate typical for the region, with high annual rainfall (2000–2500 mm) and a pronounced dry season (Malhi et al. 2009a). Mean air temperature is ca. 25 °C, with little seasonal and diurnal variation. Site climate over the study period (2009–2011) was typical for the region, with the exception of 2010 which had unusually low rainfall as part of the more widespread 2010 Amazon drought (Lewis et al. 2011). For a summary of plot characteristics, see Table 1.

In January 2002, a 1 ha area (TFR plot) was modified by the installation of plastic panels placed at ca. 2 m above the ground, excluding ca. 50% of incident rainfall. The TFR treatment caused changes in the magnitude of annual incident precipitation and dry season length and reproduced key facets of a precipitation regime typical for savannas and seasonally dry deciduous forests in South America (Betts et al. 2004; Malhi et al. 2009a) which is consistent with the long-term climate prediction for the Amazon from one major global climate model (HadCM3, Collins et al. 2001). A synthesis of stem mortality before and after natural drought events across 119 tropical forest plots in 10 countries (Phillips et al. 2010) indicated that forest near the study site showed similar drought responses to other tropical forests, and the TFR treatment produced similar responses to those observed from the larger dataset of forest responses to naturally occurring, short-term droughts. Air temperature beneath the plastic panels on the TFR plot was ca. 2 °C higher than ambient during the dry season, although soil temperature on the TFR plot remained similar

Table 1. Characteristics of the control and through-fall reduction (TFR) plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Vegetation and soil data are derived from Metcalfe et al. (2010b).

Plot characteristics	Control	TFR
Climate		
Mean annual temperature (°C)	25.8	25.8
Rainfall (mm year ⁻¹)	2311	2311
Solar radiation (GJ M ⁻² year ⁻¹)	5.7	5.7
Maximum climatic water deficit (mm month ⁻¹)	-52	-52
Vegetation		
Tree density (individuals ha ⁻¹)	434	421
Stem basal area (m ² ha ⁻¹)	23.9	24.0
Tree species diversity (species ha ⁻¹ ≥ 10 cm diameter at 1.3 m)	118	113
Soil 0–10 cm		
Clay content (%)	18	13
Silt content (%)	5	4
Sand content (%)	77	83
pH	4.0	4.0
Carbon content (g kg ⁻¹)	9	12
Nitrogen content (g kg ⁻¹)	0.4	0.3
Phosphorus content (mg dm ⁻³)	3	3
Carbon : nitrogen ratio	23	35
Soil cation exchange (cmol dm ⁻³)	0.8	0.7

to ambient values throughout. During the wet season, air temperatures above and below the TFR panels were indistinguishable (da Costa et al. 2006). The TFR treatment induced changes in plant water relations, leaf physiology and tree growth and survival (Fisher et al. 2006, 2007; da Costa et al. 2010; Metcalfe et al. 2010a). The boundary of the TFR plot was trenched to a depth of ca. 1 m and lined with plastic to minimise lateral ingress or egress of water. The perimeter of the adjacent, unmodified control plot was also trenched to avoid confounding treatment effects. All measurements were taken at least 10 m inside the perimeter of each plot to minimise edge effects. In this study, all measurements were taken over 2009–2011, unless otherwise stated.

Meteorological data

Solar radiation, air temperature, humidity and precipitation time series were collected from an automatic weather station installed in a large clearing ca. 1 km from the experimental site. Maximum climatic water deficit (MCWD), a measure of dry season intensity, was calculated, using the gap-filled monthly time series for precipitation according to the equations listed in Aragão et al. (2007).

Carbon fluxes

The protocols used to estimate ecosystem C flux components were based on those developed by the RAINFOR–GEM network. 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 2 and 3, 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, litter decomposed in the canopy, or dropped from ground flora below the litter traps. Total *R*_a is estimated:

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

Here we count root exudates and transfer to mycorrhizae as a portion of *R*_{rhizosphere} rather than as *NPP*. In quasi-steady-state conditions (and on annual timescales or longer where there no net change in plant non-structural carbohydrate storage), *GPP* should be approximately equal to *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 TFR plot, plant-level steady-state conditions may not apply. Thus, we interpret the sum of *NPP* and *R*_a in the TFR plot as *PCE* (Metcalfe et al. 2010b). Using these data, we estimated 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

The size of the TFR treatment was chosen to capture ecosystem-level responses (e.g. stand growth and respiration in mature trees) that would have been impossible to record in smaller-scale experiments (Carpenter 1996; Sullivan 1997; Osmond et al. 2004; Stokstad 2005). The disadvantage of this design was that the TFR treatment was not replicated (Hurlbert 1984, 2004) due to financial and logistical constraints. Repeated-measures analysis of variance (ANOVA) was used to test both for significant seasonal shifts in ecosystem C components, and for multi-annual shifts in *NPP*_{ACW} measured every few months since 2006, between plots. In addition, a Student's *t*-test assessed mean annual differences between the two plots. The link between stem respiration and growth was assessed with a linear regression.

All estimated fluxes reported in this study are in Mg C ha⁻¹ year⁻¹, and all reported errors show ± 1 SE. Errors

Table 2. Methods for intensive monitoring of carbon dynamics on the control and through-fall reduction (TFR) plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil (see also online supplemental material and RAINFOR–GEM manual 2012).

Component	Method description	Sampling period	Sampling interval
Above-ground net primary productivity (NPP_{AG})	Forest inventory: all trees ≥ 10 cm diameter at 1.3 m were censused within the study area in each plot to determine the growth rate of existing surviving trees, mortality and recruitment of new trees. All trees ≥ 1 cm diameter at 1.3 m within a 10×10 m ² subplot on each plot were surveyed annually to estimate the contributions of smaller stems to plot NPP_{ACW} .	2006–2011	Every year
	Seasonal growth: dendrometers were installed on all trees (≥ 10 cm diameter at 1.3 m) in each plot to measure seasonal variation in growth.	2006–2011	Every 3 months
	Branch turnover net primary productivity ($NPP_{branch\ turnover}$)	2009–2011	Every 3 months
	Litterfall net primary productivity ($NPP_{litterfall}$)	2010–2011	Every 14 days
	Leaf area index (LAI)	2009–2011	Every month
	Loss to leaf herbivory ($NPP_{herbivory}$)	2009	Every 3 months
Below-ground net primary productivity (NPP_{BG})	Coarse root net primary productivity ($NPP_{coarse\ roots}$)	n/a	Not directly measured
	Fine root net primary productivity ($NPP_{fine\ roots}$)	2009–2011	Every 3 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 and soil respiration chamber (EGM-4 IRGA and SRC-1 chamber, PP Systems, Hitchin, UK) sealed to a permanent collar in the soil. Soil surface temperature was measured with a T260 probe (Testo Ltd., Hampshire, UK) and soil moisture was recorded with a Hydrosense probe (Campbell Scientific Ltd., Logan, USA). At four points per plot, we installed pairs of plastic tubes (12 cm diameter) with one surface tube in each pair permitting both R_{soilhet} and $R_{\text{rhizosphere}}$, and the other tube in the pair inserted to 30 cm soil depth excluding $R_{\text{rhizosphere}}$. At the centre of each study area, an additional set of tubes were installed to quantify and correct for the effects of soil disturbance during tube installation.	2009–2011	Every month
	Soil CO ₂ efflux partitioned into autotrophic ($R_{\text{rhizosphere}}$) and heterotrophic (R_{soilhet}) components	This component was last directly measured at the plots in 2005 (Metcalfe et al. 2010a). In that study, leaf dark respiration was recorded for ca. 30 leaves from 15 trees per plot with a gas analyser and specialised cuvette (CIRAS 2 IRGA with PLC6 leaf cuvette, PP Systems, Hitchin, UK). Bole respiration was measured by using a closed dynamic chamber method, from 25 trees distributed evenly throughout each plot at 1.3 m height with an IRGA and soil respiration chamber (EGM-4 IRGA and SRC-1 chamber, PP Systems, Hitchin, UK) connected to a permanent collar sealed to the tree bole surface.	n/a	Not directly measured
	Above-ground live wood respiration (R_{stems})	This component of respiration was not measured directly so was estimated by multiplying 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).	2009–2011	Every month
	Coarse root respiration ($R_{\text{coarse roots}}$)		n/a	Not directly measured

Table 3. Data analysis techniques for intensive monitoring of carbon dynamics on the control and through-fall reduction (TFR) plots in the Caxiuanã National Forest Reserve, eastern Amazonia, 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 diameter at 1.3 m (cm), and H is height (m). To convert biomass values into carbon, we assumed that dry stem biomass is 47.3% carbon (Martin and Thomas 2011). 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 2012 (http://gem.tropicalforests.ox.ac.uk/page/resources) for a description of decomposition status and surface area formulas.
	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)	Hemispherical images were analysed with CAN-EYE software (https://www4.paca.inra.fr/can-eye) to calculate LAI using the 'true LAI' output from the CAN-EYE which accounts for foliage clumping, and assuming a fixed leaf inclination angle across plots.
	Loss to leaf herbivory ($NPP_{herbivory}$)	From the photographs of litterfall, leaf area with and without holes was 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.
Below-ground net primary productivity (NPP_{BG})	Coarse root net primary productivity ($NPP_{coarse\ roots}$)	See the RAINFOR-GEM manual 2012 (http://gem.tropicalforests.ox.ac.uk/page/resources) for a description and range of root:shoot ratios. In recognition of the substantial uncertainty in this estimate, we assigned a 30% error to this multiplying factor.
	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. 2007b) and used to predict root extraction beyond 40 min (up to 100 min). This approach added on average 27% and 30% to initial estimates of root mass manually extracted from cores on the control and TFR plots, respectively. 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})	Respiration rates were calculated from the linear rate of increase in CO ₂ concentration within the chamber (Metcalf 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 (Metcalf 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 tubes only in the soil surface is taken as $R_{rhizosphere}$. See online supplemental material for a more detailed description.
	Canopy respiration (R_{leaves})	To scale to canopy-level values, mean dark respiration per unit leaf area per plot from Metcalfe et al. (2010a) was multiplied by mean plot LAI in this study. To account for daytime light inhibition of leaf dark respiration, we applied the inhibition factor applied in Malhi et al. (2009b) (67% of daytime leaf dark respiration, 34% of total leaf dark respiration). These were calculated by applying the Atkin et al. (2000) equations for light inhibition of leaf respiration to a plot in Tapajós forest in Brazil (Malhi et al. 2009b; Lloyd et al. 2010). In recognition of the substantial uncertainty in this estimate, we assigned conservative error margins (30% of the mean) to the final values.
	Above-ground live wood respiration (R_{stems})	Respiration rates were calculated from the linear rate of increase in CO ₂ concentration within the chamber (Metcalf 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 dbh is bole diameter (cm) at 1.3 m height above the ground.
	Coarse root respiration ($R_{coarse\ roots}$)	See the RAINFOR-GEM manual 2012 (http://gem.tropicalforests.ox.ac.uk/page/resources) for a description and range of root:shoot ratios. In recognition of the substantial uncertainty in this estimate, we assigned a 30% error to this multiplying factor.

were propagated by taking the square root of the sum of squared absolute errors for addition and subtraction, and relative errors for division and multiplication (Taylor 1997; Malhi et al. 2009b). This assumes that uncertainties are independent and normally distributed. We explicitly consider two distinct types of uncertainty in this study. First, the sampling error associated with spatial variation in the variables measured. Second, the measurement uncertainty due to equipment functioning, measurement accuracy and, particularly, scaling localised measurement to whole-tree and whole-plot estimates. Here we assume that most *NPP* terms are measured fairly precisely and sampled without large biases, and hence *NPP* error is dominated by sampling uncertainty. In contrast, we believe that the main R_a terms include a large measurement and scaling uncertainty, though these are very difficult to directly quantify. The approach taken here is to assign explicit and conservative estimates of the combined measurement/scaling uncertainty for these components in Table 4. Some components were not directly measured at the site over the study period but were estimated from literature syntheses ($R_{\text{coarse roots}}$, $NPP_{\text{coarse roots}}$) or records from earlier in the drought treatment at the study site (R_{leaves}). In recognition of the uncertainty in these estimates, we assigned wide

errors (30% of the mean) in addition to sampling error, to these values. A description of the overall approach and assumptions made in estimating components is presented in Tables 2 and 3.

Results

Seasonal weather patterns

The study site had a strong seasonal dry period, with rainfall typically below 100 mm month⁻¹ from August to November each year (Figure 1). During this dry season, air temperature rose by ca. 2 °C while radiation increased by ca. 25%, compared with the wetter portion of the year. Relative humidity of the air remained very high throughout the year, falling to a minimum of 80% occasionally during the dry season (Figure 1).

Impacts of through-fall reduction on net primary productivity

There was no significant plot difference in $NPP_{\text{fine roots}}$, with 3.89 ± 0.80 and 3.96 ± 0.69 Mg C ha⁻¹ year⁻¹ in the control and TFR plots, respectively. By comparison, estimated $NPP_{\text{coarse roots}}$ was much lower at 0.54 ± 0.84

Table 4. Summary of carbon fluxes on the control and through-fall reduction (TFR) plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Values are presented for two periods: over 2009–2011 from the current study, and over 2005 from Metcalfe et al. 2010b (highlighted with grey). 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				TFR plot			
	Mean	Mean	Sample error	Total error	Mean	Mean	Sample error	Total error
	2005	2009–2011			2005	2009–2011		
Net primary productivity								
Leaves	2.5	2.07	0.02	0.02	2.1	1.83	0.02	0.02
Non-leaf canopy fine litter	1.1	0.87	0.03	0.03	0.7	0.74	0.02	0.02
Leaf herbivory	0.3	0.09	0.001	0.001	0.2	0.08	0.001	0.001
Branches	0.5	1.20	0.12	0.12	0.4	1.26	0.13	0.13
Stems	1.9	2.55	0.06	0.06	1.5	1.80	0.15	0.15
Coarse roots	1.1	0.54	0.08	0.84	0.2	0.38	0.06	0.59
Fine roots	3.4	3.89	0.80	0.80	2.4	3.96	0.69	0.69
Respiration								
Leaves	5.4	5.69	0.44	2.14	7.8	9.26	0.85	3.63
Stems	8.9	10.21	1.42	4.49	9.1	11.17	1.61	4.96
Coarse roots	—	2.14	0.43	3.5	—	2.35	0.48	3.83
Rhizosphere	6.2	9.93	0.63	1.63	7.3	7.61	0.71	1.47
Heterotrophic microbes	6.9	6.06	0.47	0.47	5.1	7.73	0.60	0.60
Ecosystem-level sums								
Total NPP	10.6	11.20	0.82	1.17	8.2	10.05	0.72	0.93
Above-ground NPP	6.4	6.78	0.14	0.14	4.9	5.71	0.20	0.20
Below-ground NPP	2.3	4.43	0.80	1.16	2.1	4.34	0.69	0.91
Total respiration	32.6	34.03	1.68	5.25	36.6	38.12	2.05	6.35
Autotrophic respiration	22.4	27.97	1.62	5.23	25.8	30.39	1.96	6.32
Heterotrophic respiration	10.2	6.06	0.47	0.47	10.9	7.73	0.60	0.60
GPP or PCE	33.0	39.18	1.81	5.36	33.9	40.44	2.09	6.39
CUE	0.32	0.29	0.02	0.04	0.24	0.25	0.02	0.03

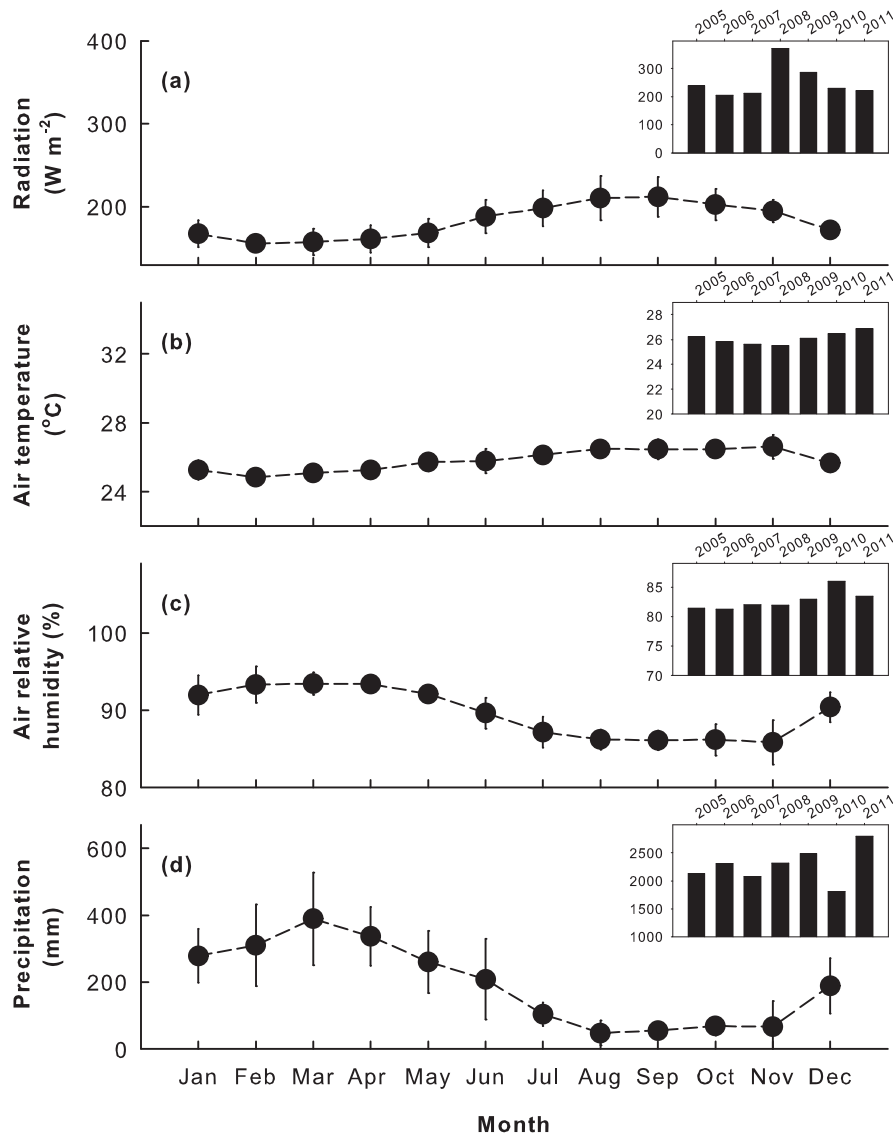


Figure 1. Seasonal (main) and annual (inset) patterns in (a) total solar radiation, (b) temperature, (c) atmospheric relative humidity and (d) precipitation recorded from a weather station near the study site in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Annual meteorology data were provided by the Tropical Ecology Assessment and Monitoring (TEAM) Network. Error bars are standard deviations.

to $0.38 \pm 0.59 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ on the control and TFR plots, respectively, though this was not recorded directly but estimated from NPP_{ACW} and a forest above-ground:below-ground biomass ratio derived from literature (Table 4, Figures 2 and 3). Both plots showed a significant ($P < 0.001$), and broadly similar, seasonal shift in $NPP_{\text{fine roots}}$, decreasing by ca. 60% from the wet to dry season (Figure 4).

Mean NPP_{ACW} was lower on the TFR plot ($1.80 \pm 0.15 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) than the control plot ($2.55 \pm 0.06 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) (Table 4; Figure 2; Figure 3). However, trees $\leq 20 \text{ cm}$ diameter at 1.3 m began to exhibit significantly higher growth rates on the TFR plot relative to the control from early 2007 onwards ($P = 0.01$; Figure 5).

The control forest canopy produced significantly ($P < 0.001$) greater quantities of fine litter (not including losses

from herbivory) ($2.94 \pm 0.04 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) than the TFR plot forest canopy ($2.57 \pm 0.03 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) (Table 4, Figures 2–4). Partitioning the annual sum into leaves and non-leaf material showed that the plot difference was mainly attributable to greater leaf fall in the control compared with the TFR plot, particularly during the dry season (Table 4). Both plots showed a similar seasonal pattern in total litter and leaf fall, increasing during the dry season, while non-leaf material production remained fairly constant throughout the year on both plots (Figure 4). $NPP_{\text{branch turnover}}$ (wood $\geq 2 \text{ cm}$ diameter) was a substantial portion of overall canopy production, at 1.20 ± 0.12 and $1.26 \pm 0.13 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ in the control and TFR plots, respectively, and showed great temporal variability but no clear, consistent seasonal cycle for either plot (Table 4, Figures 2–4).

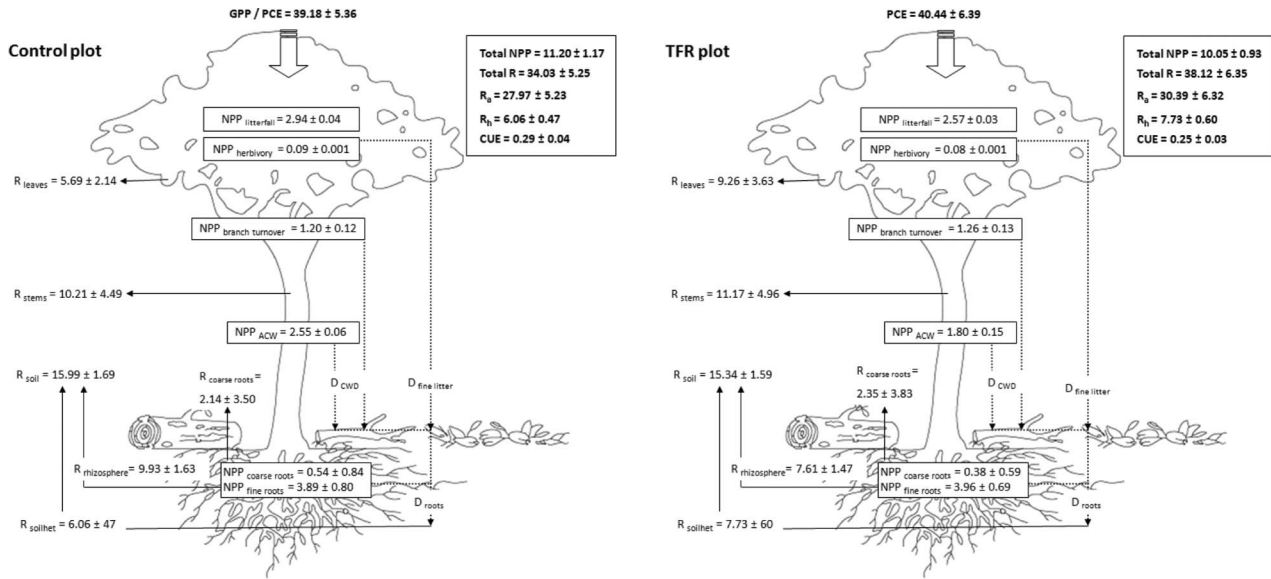


Figure 2. Diagram showing the magnitude and pattern of key carbon fluxes on the control and through-fall reduction (TFR) plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Components with prefixes *R*, *NPP* and *D* denote respiration, net primary productivity and decomposition terms respectively. Detailed descriptions of C flux components measured are presented in Tables 2 and 3. 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.

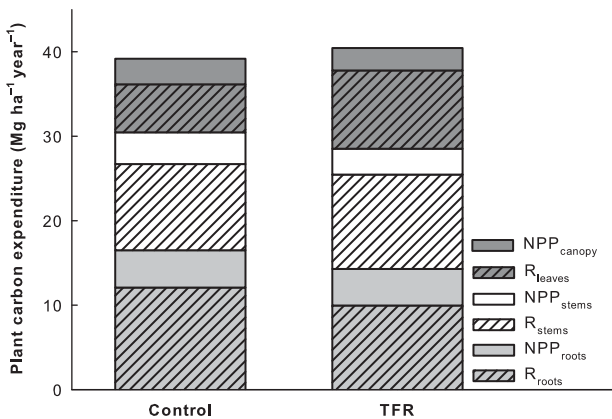


Figure 3. Allocation of plant carbon to different components on the control and through-fall reduction (TFR) plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Components with prefixes *R* and *NPP* denote respiration and net primary productivity terms, respectively. Detailed descriptions of C flux components measured are presented in Tables 2 and 3. $NPP_{canopy} = NPP_{litterfall} + NPP_{herbivory}$. $NPP_{roots} = NPP_{fine\ roots} + NPP_{coarse\ roots}$. $NPP_{stems} = NPP_{ACW} + NPP_{branch\ turnover}$. $R_{roots} = R_{rhizosphere} + R_{coarse\ roots}$.

Respiratory responses to through-fall reduction

Total *R_{soil}* was not significantly different between plots (*P* > 0.05), with annual estimates of 15.99 ± 1.69 Mg C ha⁻¹ year⁻¹ on the control plot, and 15.34 ± 1.59 Mg C ha⁻¹ year⁻¹ on the TFR plot (not including *R_{coarse roots}*) (Table 4, Figure 2) and declined progressively on both plots over the dry season (Figure 6). Annual *R_{rhizosphere}* (fine

roots and associated mycorrhizae and exudate-dependent microbes) was significantly higher (*P* < 0.001) on the control plot (9.93 ± 1.63 Mg C ha⁻¹ year⁻¹) than the TFR plot (7.61 ± 1.47 Mg C ha⁻¹ year⁻¹) (Table 4, Figures 2 and 3). This plot difference in *R_{rhizosphere}* was most accentuated in the dry season (Figure 6). By contrast, annual *R_{soilhet}* on the control plot (6.06 ± 0.47 Mg C ha⁻¹ year⁻¹) was significantly lower (*P* < 0.001) than the TFR plot (7.73 ± 0.60 Mg C ha⁻¹ year⁻¹) (Table 4, Figure 2), which was mainly driven by large plot differences in the wet–dry season transition (Figure 6). Overall, therefore, the lack of any clear treatment effect on total soil CO₂ efflux was due to the fact that the fall in *R_{rhizosphere}* on the TFR plot was offset by a rise in *R_{soilhet}*.

Mean *R_{stems}* per unit bole surface was higher on the TFR plot (1.94 ± 0.19 μmol m⁻² s⁻¹) than the control (1.61 ± 0.12 μmol m⁻² s⁻¹), though this difference was not significant. Estimated plot-level *R_{stems}* was 10.21 ± 4.49 Mg C ha⁻¹ year⁻¹ and 11.17 ± 4.96 Mg C ha⁻¹ year⁻¹ on the control and TFR plots, respectively (Table 4, Figures 2 and 3). There was no significant difference between the plots when compared on a monthly timescale.

Leaf-level trends in *R_{leaves}* were presented in Metcalfe et al. (2010a) from measurements made following 6 years of the TFR treatment. We combined these earlier leaf-level *R_{leaves}* estimates with more recent leaf area index (LAI) values of 5.5 ± 1.69 and 4.9 ± 0.20 m² m⁻² in the control and TFR plots, respectively, to estimate canopy *R_{leaves}*. The previously observed increase in leaf-level *R_{leaves}* in the TFR plot together with the relatively minor TFR-induced decline in LAI measured for the 2009–2011 period, meant

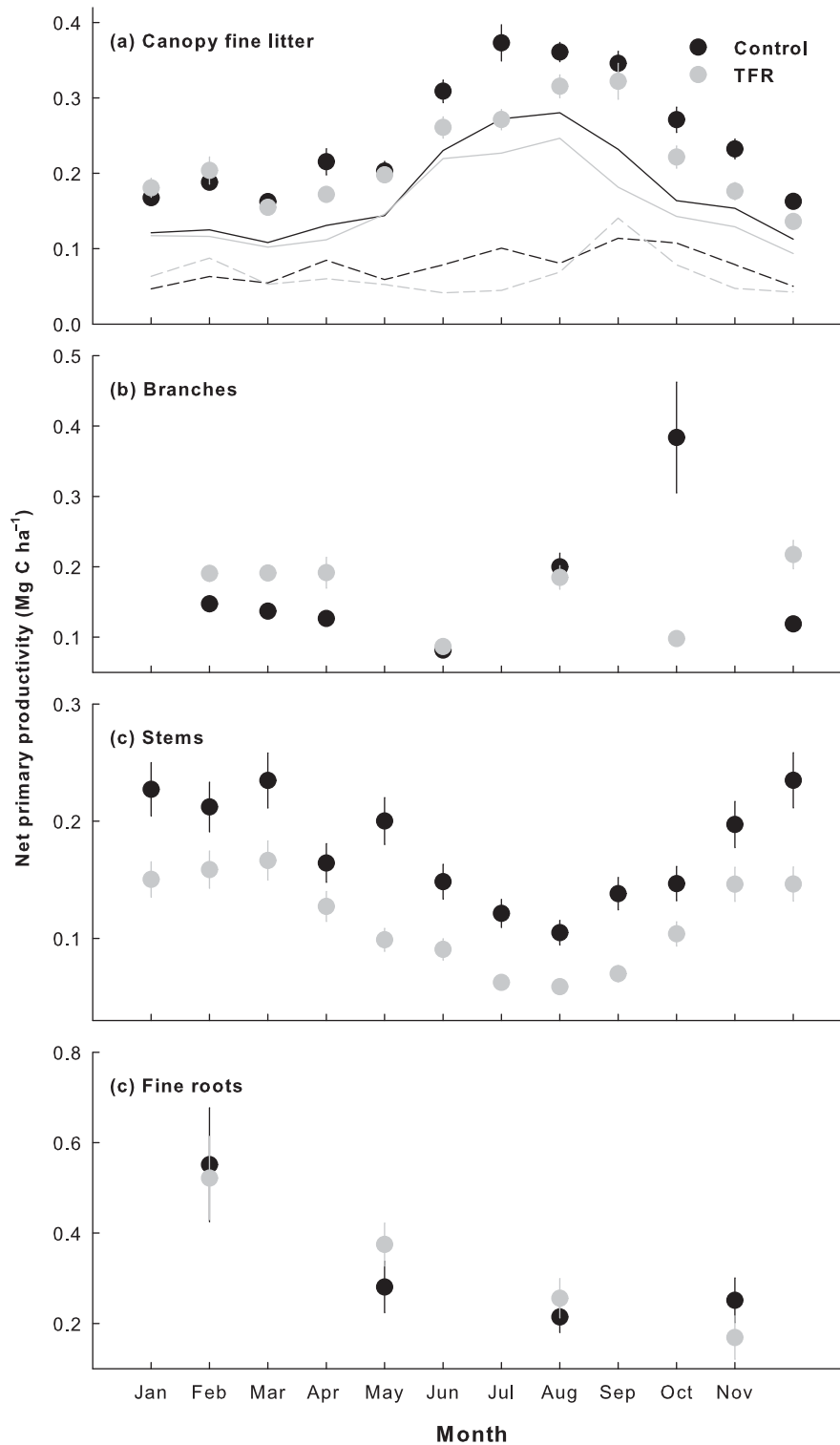


Figure 4. Seasonality of net primary productivity from canopy fine litter (a), branch turnover (b) stems (c) and roots ≤ 2 mm diameter (d) on the control and through-fall reduction (TFR) plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Canopy fine litter is subdivided into leaf material (solid lines) and non-leaf organic material (dashed lines). Non-leaf organic material includes all woody material ≤ 2 cm diameter, larger material is included in the branch turnover estimate.

that estimated total canopy R_{leaves} (day- and night-time) was substantially higher in the TFR plot (9.26 ± 3.63 Mg C ha^{-1} year $^{-1}$) than in the control (5.69 ± 2.14 Mg C ha^{-1} year $^{-1}$) (Table 4, Figures 2 and 3).

Ecosystem-level carbon processing after through-fall reduction

Total ecosystem NPP was slightly lower in the TFR plot (10.05 ± 0.93 Mg C ha^{-1} year $^{-1}$) compared with the

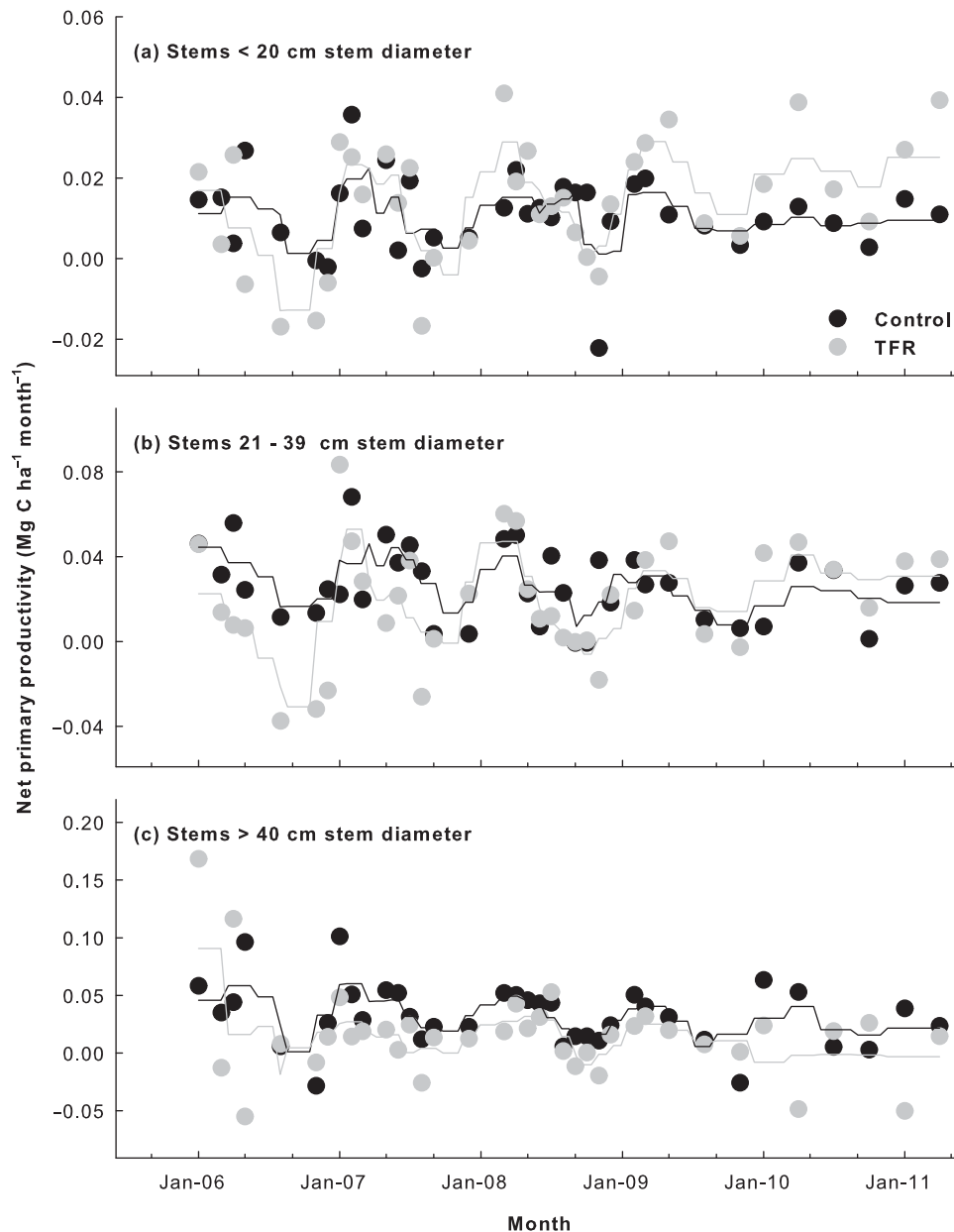


Figure 5. Monthly productivity over 6 years for stems (a) ≤ 20 cm, (b) 21–39 and (c) ≥ 40 cm diameter at 1.3 m above the ground on the control and through-fall reduction (TFR) plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Lines represent a 3-month moving average (grey, TFR; black, control).

control ($11.20 \pm 1.17 \text{ Mg C ha}^{-1} \text{ year}^{-1}$). This was entirely due to lower above-ground NPP on the TFR plot, since $NPP_{\text{fine roots}}$ actually increased slightly relative to the control (Table 4, Figures 2 and 3). Estimated R_a was ca. 9% higher on the TFR plot than the control, but there were substantial uncertainties surrounding this mean difference. Similarly, estimated total ecosystem respiration was lower on the control plot: $34.03 \pm 5.25 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ compared with $38.12 \pm 6.35 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ on the TFR plot. The net product of these changes in R_a and NPP was that estimated PCE/GPP was slightly greater, while estimated CUE was slightly lower, on the TFR plot compared with the control (Table 4, Figure 2).

Discussion

Some initial responses persist even after 10 years of through-fall reduction

The ecosystem-scale patterns of C allocation estimated in this study remained qualitatively similar to the last survey 4 years earlier in the TFR treatment (Table 4, Figure 7). The forest on the TFR plot still had lower CUE (0.25 ± 0.03) than the control (0.29 ± 0.04), as in 2005, although in the current study the plot difference was smaller and the errors were overlapping. This plot-level difference in both studies had the same underlying cause in the data: higher R_a on the TFR plot compared with the control (Table 4, Figures 2 and 3) although the magnitude of the

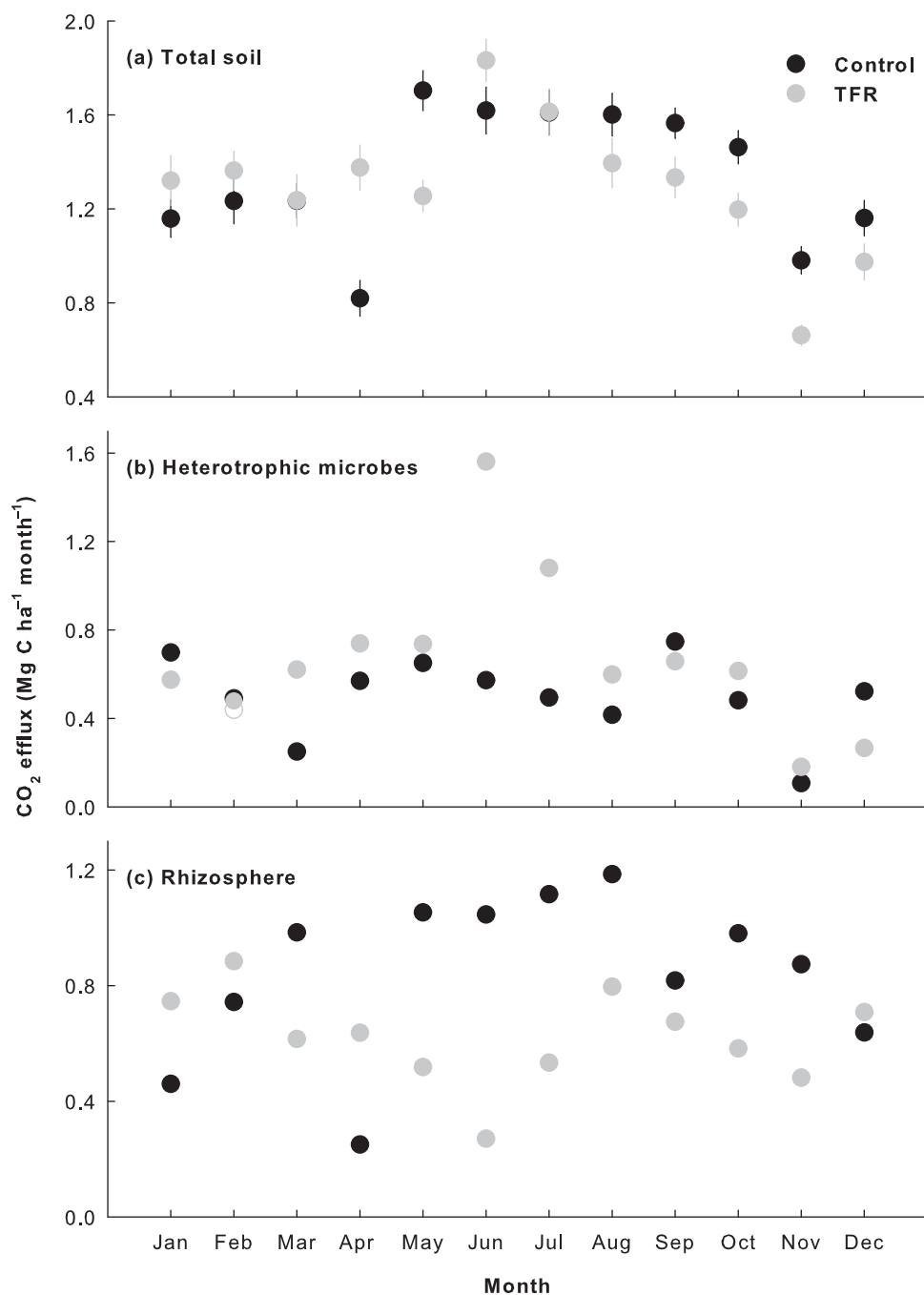


Figure 6. Seasonality of total soil CO₂ efflux (a) and contributions to this total from heterotrophic soil microbes (b) and rhizospheric sources (c) on the control and through-fall reduction (TFR) plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil. Error bars are standard errors.

TFR-induced R_a increase appeared to have decreased over time under the TFR treatment (Figure 7). However, caution is required when interpreting these apparent temporal changes because of the possible confounding impacts of differences in methods between the studies (e.g. equipment, assumptions of estimates and up-scaling approaches). In the case of $R_{\text{rhizosphere}}$, the 2005 estimate was based on *ex situ* respiration measurements on excised roots (Metcalf et al. 2007a), an approach which may have been more error prone (Makita et al. 2012) than that used in this study. Leaf-level respiration measurements were not made over

2009–2011, so the values from 2007 were applied to the 2009–2011 LAI values to derive stand-level leaf CO₂ emissions. Measurements over six leaf physiology measurement campaigns spanning the first 6 years of the TFR experiment indicated that leaf-level respiration was consistently elevated both on the TFR plot relative to the control, and on the TFR plot relative to pre-treatment values (Metcalf et al. 2010a), so it seems reasonable to assume that this difference persisted into 2009 and beyond. However, if the TFR-induced rise in leaf-level respiration has declined, or reversed since 2007, a large shift in plot estimates of R_a

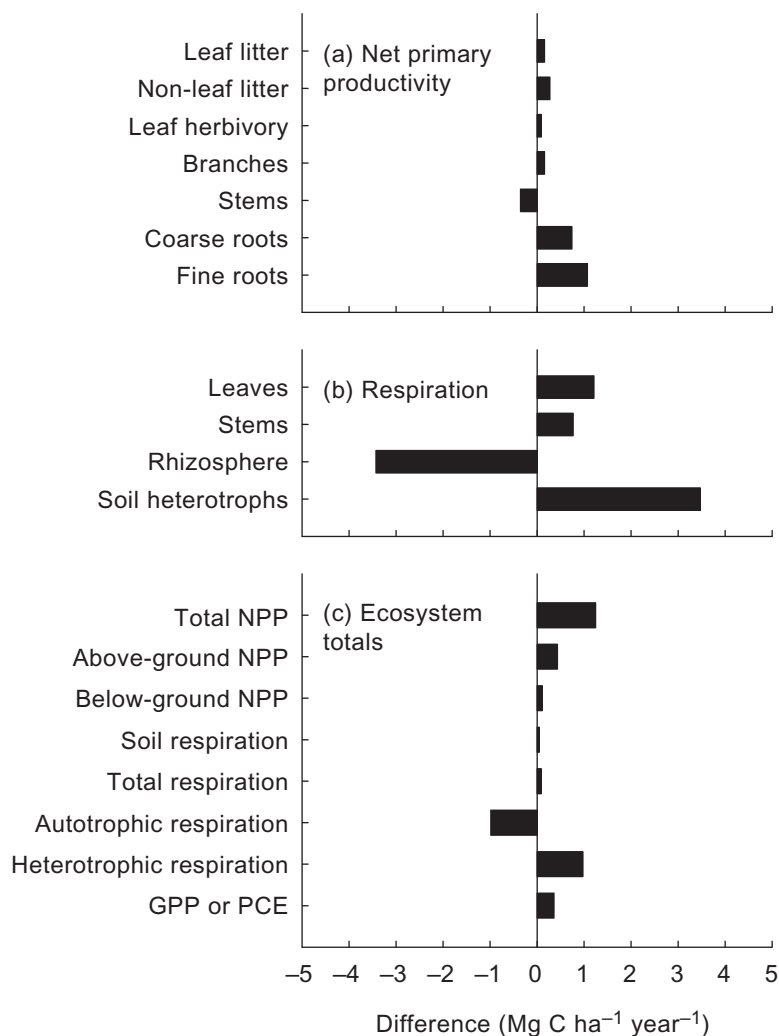


Figure 7. Net primary production (a), respiration (b) and summed ecosystem-level carbon fluxes (c) over the current study period (2009–2011) relative to measurements made 4 years earlier on the control and through-fall reduction (TFR) plots in the Caxiuanã National Forest Reserve, eastern Amazonia, Brazil (Metcalfe et al. 2010b). Changes are presented in excess of changes on the control plot over the same period of time, to remove any effects of changes in methodology between the previous study at the site and the current analysis and natural changes in climate and/or forest dynamics between 2005 and 2009–2011. *NPP*, net primary production; *GPP*, gross primary production; *PCE*, plant carbon expenditure.

would result, with *CUE* and *PCE* moving to levels closer to the control plot. We note, however, that even if TFR plot R_{leaves} was at the same level as the control, *CUE* would still be 5% lower on the TFR plot than the control, mainly due to the ca. 10% decline in *NPP* on the TFR plot relative to the control. Clearly though, further site measurements of this key component are required to test this conclusion.

As in the previous analysis at the site, the forest on the TFR plot appeared to expend slightly more C than was found for the control plot (Table 4, Figure 2), despite expectations that soil moisture deficit would cause stomatal closure and, hence, a reduction in photosynthetic C uptake (Fisher et al. 2007). Non-structural carbohydrate reserves could potentially sustain trees for some time under a net C deficit (Graham et al. 2003; Würth et al. 2005; Poorter and Kitajima 2007). Another possibility is that *GPP* partly recovered on the TFR plot. This is supported by the recovery of LAI and small tree growth on the TFR plot.

If smaller, gap-invasive trees (often characterised by leaves with high photosynthetic capacity, Chazdon et al. 1996) disproportionately benefitted from canopy gaps following elevated tree mortality on the TFR plot, this could conceivably have led to a plot-level increase in *GPP*. Smaller trees have indeed apparently benefitted from the TFR treatment, as evidenced by increased stem growth (Figure 5), but it is not known if this translates into greater canopy-level photosynthetic capacity on the TFR plot. Finally, it is possible that some portion of R_a quantified in this study and the previous synthesis at the site was actually heterotrophic, although every effort was made to avoid this error. One such misattribution could have arisen if a portion of measured R_{stems} originated from soil-sourced CO_2 transported upwards in the xylem stream (Levy et al. 1999; Teskey and McGuire 2002; Angert et al. 2012). Other potential misattributions could have operated in the opposite direction. For example, some portion of R_{soilhet} estimated with the core

exclusion partitioning method in this study may have been derived from autotrophic sources below 30 cm soil depth. However, the sum of key labile soil C inputs (litterfall + fine roots) were similar to measured R_{soilhet} on the control plot (ca. 6–7 t C ha⁻¹ year⁻¹). This suggests, firstly, that the R_{soil} partitioning method yielded broadly accurate results, secondly, that there was no large ‘missing’ heterotrophic portion of soil respiration, and thirdly, that there was no major autotrophic contribution to our R_{soilhet} estimates. Thus, it appears that xylem transport of soil CO₂ was not a major confounding at this site, although more detailed measurements (cf. Teskey and McGuire 2002; Angert et al. 2012) to directly test this preliminary conclusion are needed. Further research, refining and improving the methods outlined in this study are required to reinforce these conclusions, and test our hypotheses relating to non-structural carbohydrate reserves and plot-level GPP.

Notwithstanding the uncertainties in absolute respiration values, there was some consistency across plant tissues in terms of the direction of their respiratory response under the TFR treatment (Table 4, Figures 2 and 3). Previous work indicated that root and leaf respiration per unit tissue mass was elevated on the TFR plot (Metcalf et al. 2007a, 2010a). In this study, mean stem respiration per unit stem area was ca. 20% greater on the TFR plot than the control over the 3-year study period, although this difference was not statistically significant. The underlying physiological mechanisms for such a TFR-induced rise in specific respiration rates are unclear but the pervasive nature of the response across such different plant tissues indicates that it should be very general in nature, such as increased energy demand for the maintenance of vacuolar solute gradients, refilling of embolised xylem vessels, repair of water-stress-induced cell damage and/or increased wastage respiration via futile cycles (Hue 1982; Lambers 1997; Lambers et al. 1998; Cannell and Thornley 2000; Flexas et al. 2005; Würth et al. 2005; Wright et al. 2006; Atkin and Macherel 2009; McDowell 2011).

Overall, above-ground forest NPP was still slightly suppressed by the TFR treatment (Table 4, Figure 3) due both to lower growth per individual and, increasingly in later years of the TFR treatment, a lower stem density after several years of elevated mortality (da Costa et al. 2010). In the case of NPP_{ACW} , the suppression caused by the TFR treatment was a fairly constant offset over the year and stem growth markedly slowed on both plots over the dry season (Figure 4). $NPP_{\text{litterfall}}$ was weakly suppressed on the TFR plot but peaked on both plots during the dry season, and the magnitude of the peak was diminished on the TFR plot (Figure 4). Thus, short-term seasonally dry periods promoted litter fall on both plots but the more extended soil moisture deficit caused by the TFR treatment suppressed litterfall to some extent. More detailed measurements of $NPP_{\text{branch turnover}}$ in this study indicated that this component constituted a more substantial component of ecosystem NPP than previously appreciated (Metcalf et al. 2010b). While $NPP_{\text{branch turnover}}$ was temporally very variable, we

found evidence for enhanced $NPP_{\text{branch turnover}}$ at the dry–wet season transition on the control plot, although this could reflect forest disturbance from large storms which often signal the beginning of the wet season in the region (Figure 4). Further, these results should be interpreted with caution given that the TFR plot is not at steady-state, and so the mass of falling branches may not be an accurate proxy for $NPP_{\text{branch turnover}}$. Seasonal patterns of $NPP_{\text{fine roots}}$ recorded in this study were largely consistent with similar measurements made 4 years earlier (Metcalf et al. 2008), showing a relatively slight decline in $NPP_{\text{fine roots}}$ on the TFR plot compared with the control, and a strong, consistent decline on both plots from the wet to dry season.

Longer-term effects of through-fall exclusion begin to emerge after 7 years

While many of the overall plot differences persisted from the 2005 analysis (Metcalf et al. 2010b) to the current study, the magnitude of between-plot differences in the ecosystem-level C sums (e.g. NPP , R_a , and CUE) was generally diminished, and other individual components displayed considerable change over time under the TFR treatment (Figure 7). Most components of NPP and R_a increased from 4 to 8–10 years under the TFR treatment, with the exception of $R_{\text{rhizosphere}}$ which declined substantially on the TFR plot compared with the control, relative to the 2005 survey. By contrast, the TFR-induced rise in R_{soilhet} was much greater in 2009–2011 than 2005 (Figure 7). Total estimated PCE was substantially higher in the present study (ca. 40 Mg C ha⁻¹ year⁻¹) than the previous survey in Metcalf et al (2010b), mainly due to greater estimated R_{stems} (which was directly measured at site in the present study for the first time), $R_{\text{rhizosphere}}$ (using an improved method, not relying on potentially biased measurements from excised roots, Makita et al. 2012) and inclusion of $R_{\text{coarse roots}}$. The estimates of PCE in this study were broadly comparable with eddy flux measurements at a primary forest ca. 5 km from the study site (Carswell et al. 2002) but substantially lower than outputs from an ecophysiological model parameterised over the first 2 years of the TFR (Fisher et al. 2007).

Previous measurements at the study site showed that large trees were most sensitive to the TFR treatment, while smaller trees showed little growth response to soil moisture deficit (da Costa et al. 2010). In this study, we documented a transition ca. 2008, in the 7th year of the TFR treatment, after which smaller trees began to show a clear increase in growth on the TFR plot relative to the control (Figure 5). In a shorter-running but similar experiment also in eastern Amazonian rainforest, Brando et al. (2008) showed a similar trend 4–5 years after the imposition of the TFR treatment. We hypothesise that this pattern of response among smaller trees could reflect competitive release from competition for resources, as the elevated mortality of larger trees potentially increased the share of light, water and nutrients available to surviving trees (Wright 2002). Consistent with this, after declining by ca. 20% from 2 years after the

imposition of the TFR treatment onwards to at least early 2007 (Metcalf et al. 2010a), by 2009 onwards, LAI in the TFR plot had almost recovered to its pre-treatment level.

Overall, these results highlight the potential pitfalls of predicting future climate change impacts based upon observations from relatively short-term field experiments. Large-scale, long-term experiments, such as the TFR experiment in this study, are difficult to maintain and replicate but remain crucial for our understanding of global change phenomena because they present a unique opportunity to examine the net product of higher order interactions between multiple ecosystem components at the spatial and temporal scales most relevant for environmental models (Leuzinger et al. 2011). The TFR experiment only simulated one key component of real drought – soil moisture deficit – and the treatment effects overlie natural rainfall variability in the region. For example, in the middle of the study period the region experienced a natural drought (Lewis et al. 2011, Figure 1). The interactive effects of natural and treatment-induced moisture deficit, and other variables which often change under natural drought (e.g. air temperature and humidity), remain an important topic for further research. Our efforts are now focused on fusing the ecosystem-level C budget at the site with more controlled experimental studies of individual ecosystem components (e.g. non-structural carbohydrates, leaf respiration), and climate models (e.g. Marthews et al. 2012) to develop a more robust, integrated picture (Luo et al. 2011) of the fate of Amazon forests under future climate change.

Conclusion

This study presents a detailed overview of ecosystem carbon cycling after 8 years in the longest-running large-scale tropical TFR experiment. The results provide unique insights into the long-term impacts of drought at a spatial and temporal scale most relevant for understanding of ecosystem-level responses. Our findings largely reinforce the key results of a similar survey 4 years earlier in the TFR treatment: that *NPP* declines but R_a rises on the TFR plot relative to the control, though the plot differences are much smaller than before. The consequences of these shifts are that the forest itself apparently experiences a weak reduction in *CUE*, and the pattern of C cycling on the TFR plot is shifted to a state where it is more likely to be a net source of CO_2 because of reduced *NPP* and increased R_a . Further work remains to improve the accuracy of these estimates, especially for some key plant respiration terms. It is also important to assess how well these responses to experimental TFR represent the impacts of real drought events across the Amazon, and other tropical forests, and thus to more fully evaluate the implications for model simulations of Amazon ecosystem responses to future climate change.

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