

Plant Ecology & Diversity

Publication details, including instructions for authors and subscription information:
<http://www.tandfonline.com/loi/tped20>

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Published online: 18 Sep 2013.

To cite this article: Alejandro Araujo-Murakami, Christopher E. Doughty, Daniel B. Metcalfe, Javier E. Silva-Espejo, Luzmila Arroyo, Juan P. Heredia, Marcio Flores, Rebeca Sibler, Luz M. Mendizabal, Erwin Pardo-Toledo, Meison Vega, Luzmarina Moreno, Victor D. Rojas-Landivar, Kate Halladay, Cecile A.J. Girardin, Timothy J. Killeen & Yadvinder Malhi, Plant Ecology & Diversity (2013): The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia, Plant Ecology & Diversity, DOI: 10.1080/17550874.2013.798364

To link to this article: <http://dx.doi.org/10.1080/17550874.2013.798364>

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The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia

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(Received 13 March 2012; final version received 18 April 2013)

Background: The dry transitional forests of the southern Amazonia have received little attention from a carbon cycling and ecosystem function perspective, yet they represent ecosystems that may be impacted by global climate change in the future.

Aims: To compare the full carbon cycle for two 1-ha forest plots that straddle the ecotone between humid forest and dry forest in Amazonia, ca. 100 km from Santa Cruz, Bolivia.

Methods: 2.5 years of measurements of the components of net primary production (NPP) and autotrophic respiration were collected.

Results: Total NPP was 15.5 ± 0.89 Mg C ha⁻¹ year⁻¹ at the humid site and 11.27 ± 0.68 Mg C ha⁻¹ year⁻¹ at the dry site; a total Gross Primary Production (GPP) of 34.14 ± 2.92 Mg C ha⁻¹ year⁻¹ and 26.88 ± 2.70 Mg C ha⁻¹ year⁻¹ at the two sites. Carbon use efficiency for both sites was higher than reported for other Amazonian forests (0.45 ± 0.05 and 0.42 ± 0.05).

Conclusions: Drier soil conditions selected for the dry deciduous tree species which had higher leaf photosynthesis and total GPP. NPP allocation patterns were similar at the two sites, suggesting that in terms of carbon allocation, the dry forests of the southern Amazonia behave as a scaled-down version of wetter humid forests.

Keywords: Bolivia; CUE; GPP; NPP; respiration; seasonally dry tropical forest

Introduction

The humid forests of eastern Bolivia have been expanding southward over the past 3,000 years and their present-day location may represent the southernmost extent of Amazonian rain forest over the past 50,000 years (Mayle et al. 2000). Long-term sediment cores from Lake Titicaca indicate that southern Amazonia may have experienced a dry period 8,000–5,500 years ago during a time of low summer insolation (Baker et al. 2001). Because the Southern Amazon region is prone to changes in precipitation, the southernmost Amazonian forests of Bolivia may be among those most affected by future changing climatic conditions.

However, the carbon cycle in dry southern Amazonian forests has been less well studied than the more humid central and eastern Amazon, where most large-scale carbon cycling measurements have taken place (Malhi et al. 2009b; Davidson et al. 2012). This is important because the carbon dynamics of these southern Amazonian transition forests may shift in the future due to changing rainfall or the result of fire. Rainfall in this region may decrease in the future in response to climate warming (Malhi et al. 2008) or increases in global or regional albedo. Rainfall patterns have shifted in the past due to changing orbital parameters which change the solar insolation absorbed by

South America (Cruz et al. 2005). Recent modelling studies have indicated that precipitation in this region is sensitive to albedo shifts from northern hemisphere afforestation (Swann et al. 2012) or large-scale increases in South American albedo from deforestation (Doughty et al. 2012).

This region, and much of Amazonia, experienced large droughts in 2005 and 2010 (Lewis et al. 2011). The 2005 drought was hailed as a potentially once-in-a-century event and the second such event within five years might signify a change in the climate system (Marengo et al. 2008; Saatchi et al. 2013). This transition forest zone is also likely to experience fires on a regular basis, and the frequency of fires is likely to increase as land use pressure increases (Nepstad et al. 1999; Alencar et al. 2005). However, the effect of drought and other disturbances on carbon cycling in tropical forests is currently not well understood. Ongoing multi-year drought disturbance, such as that simulated in a 1 ha rain exclusion experiment in humid eastern Amazonia have been shown to lower carbon use efficiency in tropical forests (Metcalfe et al. 2010). In contrast, however, single disturbance drought events may increase carbon use efficiency since more carbon is allocated to biomass production during the recovery phase (Malhi et al. 2009b).

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In order to improve the understanding of carbon cycling in humid dry transition forest zones we therefore initiated an intensive study of the carbon cycle in Bolivia. Above-ground biomass has been estimated in southern Amazonian forests (Malhi et al. 2006), but there has been no work carried out on other important aspects of the carbon cycle, such as net primary production (NPP) or carbon use efficiency (CUE) (Malhi et al. 2009b). NPP is typically measured in the field by the summing the production rates of biomass (wood, leaves and fine roots). There is now a large dataset on canopy and woody growth in the tropics, but root production is rarely measured in parallel with the above-ground components (Malhi et al. 2011). A recent review of allocation of NPP in tropical forests has shown that allocation patterns were fairly consistent across sites, with little variance in canopy allocation but shifting allocation between fine roots and woody tissue NPP (Malhi et al. 2011).

Carbon use efficiency is expressed as the ratio of Net Primary Production (NPP) to GPP, or the percentage of fixed carbon that is allocated to growth. To measure CUE at the stand level, all aspects of NPP and autotrophic respiration must be accounted for. An early study by Chambers et al. (2004) found that CUE near Manaus averaged 0.3, which is lower than the value of 0.5 typical to temperate forests (Chambers et al. 2004). It appears that a lower CUE figure is with a feature of old-growth systems and a higher CUE is associated with either recovery from disturbance or with systems that are naturally more dynamic (De Lucia et al 2007; Malhi et al. 2009a).

In the present paper, we present data on multiple aspects of the carbon cycle from two 1 ha plots in the forests of the Bolivian Amazon. The plots were located in the transition zone between the humid Amazon forest and the *chiquitano* transition forest, and differed in terms of their physiognomy and floristic composition. One of the plots had drainage characteristics (shallow soils) that supported xeric or dry deciduous trees more characteristic of dry *chiquitano* forests, and the other had drainage characteristics leading to species more typical of humid Amazonian forests. The study compared the patterns of productivity, respiration and carbon allocation in these two plots and addressed the following specific questions:

1. How do the seasonal cycles of the components of autotrophic respiration and NPP vary between the two plots?

2. What is the total budget of NPP and respiration, and how does this budget vary between the more humid and more xeric plot?
3. Do carbon allocation patterns and CUE differ between the more humid and more xeric plot?

Materials and methods

Site characteristics

Two 1 ha plots (100 × 100 m) were established and monitored on private property at the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia (16.0158° S, 62.7301° W) from January 2009. The plots were 2 km apart and were situated on inceptisols with relatively high fertility (high cation exchange capacity and phosphorus concentration), compared with eastern Amazonian forests (Quesada et al. 2011) and low acidity (Table 1). The plots experienced almost identical climate and had sandy loam soil with 76% sand content (Table 1). However, one plot was located on shallow soil (<1 m depth) over Precambrian bedrock, leading to less available water (we term this plot, Kenia-dry). The second plot was located on deeper soils in a slight topographic depression (termed Kenia-wet). These differences in drainage and soil depth had an effect on forest composition at this ecotone, with Kenia-wet hosting a more humid and Kenia-dry a drier forest type.

Kenia-wet contained large trees, with lower wood density and large leaves typical of the Amazon biome, including several species and genera with a wide Amazonian distribution such as *Cariniana* spp., *Ceiba pentandra*, *Ficus* spp., *Hura crepitans*, *Pesudolmedia laevis*, *Schizolobium amazonicum* and *Swietenia macrophylla*. Kenia-dry had trees of generally higher wood density, with thorny branches and small leaves, including species such as *Anadenanthera macrophylla*, *Caesalpinia pluviosa*, *Piptadenia viridiflora* and *Swetia fruticosa*, typical of the dry *chiquitano* forest region which borders the humid Amazon forest zone. These two plots, although only 2 km apart, could therefore be considered ecologically to straddle the humid forest – dry forest ecotone.

As with many dry forests, the forests in this area are subject to periodic ground fires. The region containing our plots experienced a fire in 2004, ca. 5 years before the start of the measurements (authors' personal observation). This was a low intensity blaze that burned the understorey and left fire scars on the trees, but did not kill many of the larger trees in either of the plots.

Table 1. Soil characteristics from Kenia-wet and Kenia-dry, Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia, in November 2010 which are averages from five locations per plot at four soil depths (organic layer, 0–10 cm, 10–20 cm, 20–30 cm). Samples were analysed in the Laboratory of Soils, Water and Plants, Universidad Autónoma Gabriel Rene Moreno, Santa Cruz, Bolivia, April 2011. Asterisks represent significant differences ($P < 0.01$) between the plots.

	Sand (%)	Silt (%)	Clay (%)	pH	Na (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	P (ppm)	N (ppm)	Soil physics
Kenia-wet	76 ± 2	8 ± 1	16 ± 2	6.2 ± 0.6**	97	217**	2045	249	1.2	2460	sandy loam
Kenia-dry	76 ± 5	8 ± 4	16 ± 5	5.0 ± 1	105	120	1235	194	2.4**	2361	sandy loam

Carbon fluxes

The protocols used to estimate ecosystem Carbon-flux components within the 1 ha plot (divided into 25 20×20 m² subplots) were largely based on those developed by the RAINFOR–GEM network. Measurements were distributed evenly through the plot, approximately one per subplot (except for ingrowth cores, which at $N = 16$, were at the corners of subplots). A detailed description is available online for downloading (<http://gem.tropicalforests.ox.ac.uk>) and in the online Supplementary 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, and litter decomposed in the canopy. Total R_a (autotrophic respiration) is estimated as

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

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

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

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

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

Meteorological data

Solar radiation, air temperature, relative humidity and precipitation were collected from an automatic weather station (AWS) (Skye Instruments, Llandrindod, UK) at a site about 1 km from the plot (detailed meteorological methodology in the online Supplementary Material). The original data were measured with at least 30-minute resolution for the period between January 2009 and March 2011. Soil moisture content in the top 18 cm was also measured monthly at 25 locations per plot using a Hydrosense probe (Campbell Scientific Ltd., Loughborough, UK).

Statistics and error analysis

A key consideration was the assignment and propagation of uncertainty in our measurements. We identified two primary types of uncertainty. Firstly, there was sampling uncertainty associated with the spatial heterogeneity of each study plot and the limited number of samples per plot. Examples included the variability among litter traps, or among fine root ingrowth cores. Secondly, there was a systematic uncertainty associated with either unknown biases in measurement, or uncertainties in scaling measurements to the plot level. Examples of unknown biases included the possibility of soil CO₂ in the transpiration stream affecting the stem and CO₂ efflux measurements, and uncertainties in scaling included the allometry of scaling of bole stem CO₂ efflux to whole tree stem respiration, or leaf dark respiration to whole canopy dark respiration. We have assumed that most NPP terms were measured fairly precisely and sampled without large biases: hence the NPP component measurements were dominated by sampling uncertainty, which can be reliably estimated assuming a normal distribution. On the other hand, some of the main autotrophic respiration terms were likely to have been dominated by systematic uncertainty. Systematic uncertainty can be very difficult to quantify reliably, and in each case we made an explicit and conservative estimate of the systematic uncertainty of key variables ([Table 3](#)).

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

Results

Meteorology

The site exhibited a strong seasonality in rainfall, ranging from over 200 mm month⁻¹ at the peak of the rainy season (December to February) to less than 100 mm month⁻¹ between April and September ([Figure 1\(d\)](#)). The dry season length is frequently defined as the number of months with < 100 mm rainfall month⁻¹, 100 mm being the typical monthly water loss through evapo-transpiration in tropical forests (Fisher et al. 2009). By this definition the site experienced a six-month dry season, this being the limit that is able to sustain humid tropical forest (Malhi and Wright 2004). There was a bimodal peak in solar radiation, because solar radiation was reduced by wet season cloudiness in December–February, while in May–September it was reduced due to the austral winter.

There was also seasonality in air temperature, the coldest temperatures occurring in May–July (austral winter), during which there were occasional incursions by polar

Table 2. Methods for intensive studying of carbon dynamics in Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia (see also supplementary material and RAINFOR-GEM manual 2012).

Component	Description	Sampling period	Sampling interval
Above-ground net primary productivity (NPP_{AG})	Forest inventory: All trees ≥ 10 cm DBH censused to determine growth rate of existing surviving trees and rate of recruitment of new trees. Stem biomass calculated using the Chave et al. (2005) allometric equation for tropical moist forests, employing diameter, height and wood density data. Four 10×10 m ² sub-plots were established to carry out censuses on small trees (2.5–10 cm DBH) using calipers and data was scaled up to one hectare. Seasonal growth: Dendrometers were installed on all trees > 10 cm DBH in each plot to determine the spatial-temporal and seasonal variation in growth.	2008–2010	Every year (trees ≥ 10 cm DBH) Every six months (trees 2.5–10 cm DBH)
Branch turnover net primary productivity ($NPP_{branch\ turnover}$)	Branches (excluding those fallen from dead trees) were surveyed within four 1×100 m ² transects; small branches were cut to include only the transect-crossing component, removed and weighed. Larger branches had their dimensions taken (diameter at three points) and all were assigned a wood density value according to their decomposition class.	2008–2010 2009–2011	Every month Every month
Litterfall net primary productivity ($NPP_{litterfall}$)	Litterfall production of dead organic material less than 2 cm diameter was estimated by collecting litterfall in 0.25 m ² (50×50 cm ²) litter traps placed at 1 m above the ground at the centre of each of the 25 sub-plots in each plot.	January 2009–June 2011	Every month
Leaf area index (LAI)	Canopy images were recorded with a digital camera and hemispherical lens near the centre of each of the 25 sub-plots in each plot, at a standard height of 1 m, and during overcast conditions. LAI was estimated from these images using CAN-EYE (Demarez et al. 1996) software.	January 2009–June 2011	Every month
Loss to leaf herbivory ($NPP_{herbivory}$)	We employed data on the fraction of canopy leaf area that is lost to herbivory ($18.8 \pm 1.3\%$) collected from two forest plots in Tambopata, Madre de Dios, SE Peru, plots with similar carbon cycle properties to the site reported here. We multiplied this fractional herbivory with the annual leaf litterfall measured here to estimate total herbivory.	n/a	Not directly measured
Below-ground net primary productivity (NPP_{BG})	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 ($NPP_{\text{fine roots}}$)	Sixteen ingrowth cores (mesh cages 14 cm diameter, installed to 30 cm depth) were installed in each plot. Cores were extracted and roots were manually removed from the soil samples in four 10 min time steps and the pattern of cumulative extraction over time was used to predict root extraction beyond 40 min. Root-free soil was then re-inserted into the ingrowth core. Collected roots were thoroughly rinsed, oven dried at 80 °C, and weighed.	November 2008–March 2011	Every 3 months
Autotrophic and heterotrophic respiration	Total soil CO_2 efflux (R_{soil})	January 2009–June 2011	Every month
	Soil CO_2 efflux partitioned into autotrophic ($R_{\text{rhizosphere}}$) and heterotrophic (R_{soilhet}) components	February 2009–June 2011	Every month
	Canopy respiration (R_{leaves})	November 2010 and July 2011	Once in dry season, once in wet season
	Above-ground live wood respiration (R_{stems})	March 2009–December 2010	Every 2 months
	Coarse root respiration ($R_{\text{coarse roots}}$)	n/a	Not directly measured

Table 3. Data analysis techniques for intensive studying of carbon dynamics in Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia (see also supplementary material and RAINFOR-GEM manual 2012).

	Component	Data processing details
Above-ground net primary productivity (NPP_{AG})	Above-ground coarse wood net primary productivity (NPP_{ACW})	Biomass calculated using the Chave <i>et al.</i> (2005) allometric equation for tropical moist forests: $AGB = 0.0509 \times (\rho D H)$ where AGB is aboveground biomass (kg), ρ is density (g cm^{-3}) of wood, D is DBH (cm), and H is height (m). To convert biomass values into carbon, we assumed that dry stem biomass is 47.4% carbon (Martin and Thomas 2011).
	Branch turnover net primary productivity ($NPP_{\text{branch turnover}}$)	See RAINFOR-GEM manual (Version 2.2, 2012, p.61) for description.
	Litterfall net primary productivity ($NPP_{\text{litterfall}}$)	$NPP_{\text{litterfall}}$ is calculated as follows: $NPP_{\text{litterfall}} = NPP_{\text{canopy}} - \text{loss to leaf herbivory}$. Litterfall is separated into different components, oven dried at 80 °C to constant mass and weighed. Litter is estimated to be 49.2% carbon, based on mean Amazonian values (S. Patiño, unpublished analysis).
	Leaf area index (LAI)	LAI estimated using 'true LAI' output from the CAN-EYE program which account for clumping of foliage, and assuming a fixed leaf inclination angle of 42.5°, based on average estimates at Kenia-wet. Leaves were separated into sunlit and shaded fractions using the following equation: $F_{\text{sunlit}} = (1 - \exp(-K \cdot \text{LAI}))/K$, 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°.
Below-ground net primary productivity (NPP_{BG})	Loss to leaf herbivory ($NPP_{\text{herbivory}}$)	The fractional herbivory (H) for each leaf was then calculated as: $H = (A_{\text{nh}} - A_{\text{h}}) / A_{\text{nh}}$, 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.
	Coarse root net primary productivity ($NPP_{\text{coarse roots}}$) Fine root net primary productivity ($NPP_{\text{fine roots}}$)	See RAINFOR-GEM manual (Version 2.2, 2012, p.47) for description of root:shoot ratio. 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 <i>et al.</i> 2007) and used to predict root extraction beyond 40 min (up to 100 min); we estimate that there was an additional 28% correction factor for fine roots not collected within 40 min. Correction for fine root productivity below 30 cm depth increased the value by 39%.
Autotrophic and heterotrophic respiration	Total soil CO ₂ efflux (R_{soil})	Soil surface temperature (T260 probe, Testo Ltd., Hampshire, UK) and moisture (Hydrosense probe, Campbell Scientific Ltd., Loughborough, UK) were recorded at each point after efflux measurement.
	Soil CO ₂ efflux partitioned into autotrophic ($R_{\text{rhizosphere}}$) and heterotrophic (R_{soilhet}) components	The partitioning experiment allows estimation of the relative contributions of (1) roots, (2) mycorrhizae and (3) soil organic matter to total soil CO ₂ efflux. Contributions are estimated from differences between collars subjected to different treatments, in excess of pre-existing spatial variation. In recognition of the substantial uncertainty in this estimate, we assigned a 10% error to the multiplying factor.
	Canopy respiration (R_{leaves})	To scale to whole-canopy respiration, mean dark respiration for shade and sunlit leaves were multiplied by the respective estimated fractions of total LAI. 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 <i>et al.</i> (2009b) (67% of daytime leaf dark respiration, 33% of total leaf dark respiration) (Atkin <i>et al.</i> 2000). In recognition of the substantial uncertainty in this estimate, we assigned a 30% error to the multiplying factor.

(Continued)

Table 3. (Continued).

Component	Data processing details
Above-ground live wood respiration (R_{stems})	To estimate plot-level stem respiration tree respiration per unit bole area was multiplied by bole surface area (SA) for each tree, estimated with the following equation (Chambers et al. 2004): $\log(SA) = -0.105 - 0.686 \log(DBH) + 2.208 \log(DBH)^2 - 0.627 \log(DBH)^3$, where H is tree height, and DBH is bole diameter at 1.3 m height. Finally, for all 25 trees together we regressed mean annual bole respiration against total annual growth. In recognition of the substantial uncertainty in this estimate, we assigned a 30% error to the multiplying factor.
Coarse root respiration ($R_{\text{coarse roots}}$)	In recognition of the substantial uncertainty in this estimate, we assigned a 50% error to the multiplying factor.

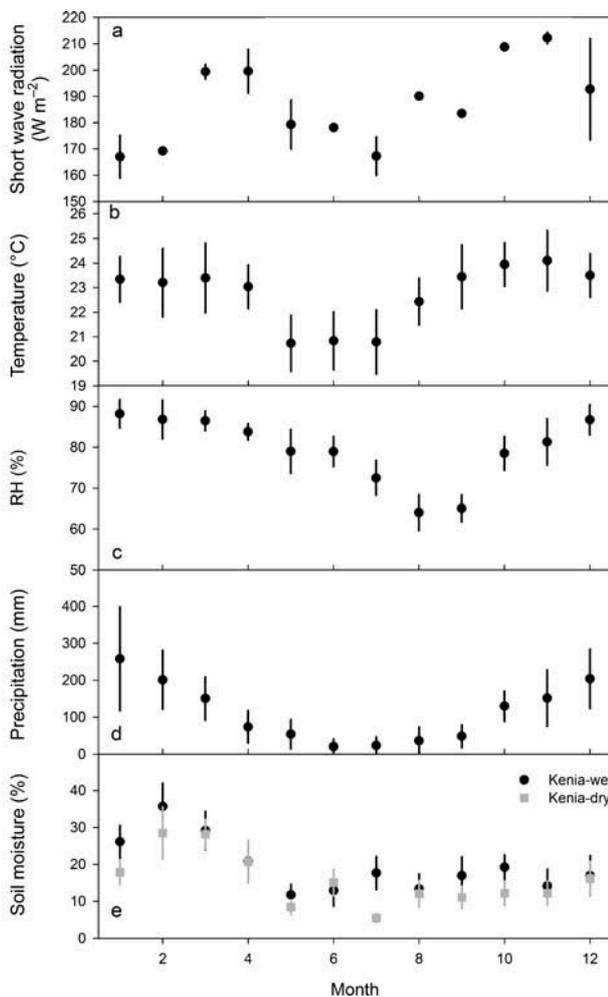


Figure 1. Climate data from a meteorological station for (a) total radiation (W m^{-2}), (b) average monthly temperature ($^{\circ}\text{C}$), (c) relative atmospheric humidity (RH, water vapour/ saturated water vapour), (d) average monthly precipitation (mm month^{-1}), and (e) average soil moisture (%) in the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia. Error bars are standard deviations of monthly mean values.

fronts (called *surazos* in Bolivia) which could cause temperatures to dip as low as 5°C . These lasted only a few days and caused the mean monthly winter temperature to dip by $1\text{--}2^{\circ}\text{C}$ (Figure 1(b)). Atmospheric relative humidity was

lowest in the late dry season (August–September), when moisture supply was low and temperatures were high. The mean annual air temperature was ca. 23.4°C .

The mean annual rainfall over the period 2005–2011 was ca. 1310 mm; this is likely to be lower than the long-term mean due to droughts in 2005 and 2010. Soil moisture content in the top 30 cm measured monthly at 25 locations per plot (Figure 1(e)) was significantly higher ($P < 0.001$) in Kenia-wet ($19.7 \pm 0.38\%$) than in Kenia-dry ($16.0 \pm 0.34\%$ water).

Fine root NPP

In the initial excavation we measured fine root stocks and found no significant difference between Kenia-wet ($8.18 \pm 1.43 \text{ Mg C ha}^{-1}$) and Kenia-dry ($6.07 \pm 1.33 \text{ Mg C ha}^{-1}$). Kenia-wet had significantly more total fine root NPP ($P < 0.001$) than Kenia-dry, averaging $0.30 \pm 0.013 \text{ Mg C ha}^{-1} \text{ month}^{-1}$, against an average of $0.23 \pm 0.008 \text{ Mg C ha}^{-1} \text{ month}^{-1}$ for Kenia-dry.

On a seasonal scale, fine root NPP (Figure 2) was 61% higher in February than in August in Kenia-wet, and 37% higher in February than in August in Kenia-dry.

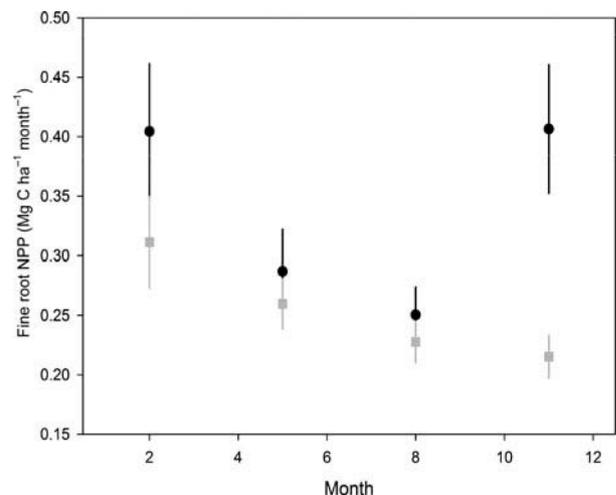


Figure 2. Fine root NPP ($\text{Mg C ha}^{-1} \text{ month}^{-1}$) from 16 ingrowth cores collected every three months over a 2-year period for the Kenia-wet (black) and Kenia-dry (grey) plots in the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia. Error bars are standard errors.

Table 4. Total yearly averaged canopy NPP, components of canopy NPP, herbivory, branch NPP, aboveground wood NPP, coarse root NPP, fine root NPP, canopy respiration, stem respiration, rhizosphere respiration, coarse root respiration, soil heterotrophic respiration, total autotrophic respiration, NPP, GPP and CUE for 2.5 years of data for plots Kenia-wet and Kenia-dry, our two study plots in the Hacienda Kenia in Guarayos Province, near Santa Cruz, Bolivia. Units are all $\text{Mg C ha}^{-1} \text{ year}^{-1}$. Sample error is uncertainty associated with the spatial heterogeneity of the study plot and the limited number of samples. Total error is sampling error plus an estimate of systematic uncertainty associated with either unknown biases in measurement, or uncertainties in scaling measurements to the plot level.

	Kenia-wet Mean	Sample error	Total error	Kenia-dry Mean	Sample error	Total error
NPP_{canopy}	5.65	0.65	0.65	4.23	0.57	0.57
NPP_{leaf}	2.91	0.30	0.30	2.22	0.25	0.25
NPP_{flower}	0.24	0.09	0.09	0.12	0.07	0.07
NPP_{fruit}	0.40	0.19	0.19	0.32	0.23	0.23
NPP_{twigs}	1.33	0.33	0.33	1.10	0.32	0.32
Herbivory	0.55	0.06	0.06	0.42	0.05	0.05
NPP_{seeds}	0.07	0.14	0.14	0.07	0.25	0.25
$NPP_{\text{branch turnover}}$	0.57	0.06	0.06	0.58	0.06	0.06
$NPP_{\text{ACW} > 10\text{cm dbh}}$	2.71	0.27	0.27	2.10	0.21	0.21
$NPP_{\text{ACW} < 10\text{cm dbh}}$	1.41	0.14	0.14	0.46	0.05	0.05
$NPP_{\text{coarse roots}}$	0.57	0.06	0.06	0.44	0.04	0.04
$NPP_{\text{fine roots}}$	4.04	0.51	0.51	3.04	0.28	0.28
R_{leaf}	5.23	0.55	1.59	4.43	0.35	1.24
R_{stem}	7.44	0.90	3.14	7.26	0.99	3.16
$R_{\text{rhizosphere}}$	4.40	0.55	0.99	2.40	0.29	0.53
$R_{\text{coarse root}}$	1.56	0.19	0.19	1.52	0.19	0.19
$R_{\text{soil het}}$	8.47	0.98	0.98	9.51	1.37	1.37
$R_{\text{autotrophic}}$	18.64	1.21	2.78	15.61	1.10	2.61
NPP	15.50	0.89	0.89	11.27	0.68	0.68
GPP	34.14	1.50	2.92	26.88	1.30	2.70
CUE	0.45	0.03	0.05	0.42	0.03	0.05

higher in Kenia-dry. Kenia-wet had significantly more roots than Kenia-dry ($P < 0.01$) (Figure 2). Total average annual fine root growth for Kenia-wet was $4.04 \pm 0.51 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ and $3.04 \pm 0.28 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-dry (Table 4).

Above-ground woody NPP

We measured woody NPP for small trees (between 2.5 and 10 cm DBH) in a $20 \text{ m} \times 20 \text{ m}$ subplot of our 1-ha plot. At Kenia-wet there were 48 small stems in the subplot with an average NPP of $0.31 \text{ Mg C ha}^{-1} \text{ year}^{-1}$. At Kenia-dry, there were 72 stems with an average NPP of $0.49 \text{ Mg C ha}^{-1} \text{ year}^{-1}$. At Kenia-wet, there were many *Heliconia* sp. (a common large-leaved banana-like understorey plant), whose NPP was difficult to measure using our normal techniques. In a subsample, we measured the NPP as $1.12 \text{ Mg C ha}^{-1} \text{ year}^{-1}$, which we added to NPP for small trees at Kenia-wet (detailed in the online supplemental material).

Average wood density was 0.60 g cm^{-3} and 0.63 g cm^{-3} at the wet and dry sites, respectively. There were no significant differences in tree stature. Mean tree height for trees $< 20 \text{ cm DBH}$ was $9.6 \pm 3.6 \text{ m}$ (wet) and $10.2 \pm 1.6 \text{ m}$ (dry), for trees $20\text{--}40 \text{ cm DBH}$ the figures were $16.3 \pm 4.3 \text{ m}$ and $16.5 \pm 4.4 \text{ m}$, and for trees $> 40 \text{ cm DBH}$ they were $21.6 \pm 5.1 \text{ m}$ and $22.9 \pm 3.3 \text{ m}$.

Total stand level above-ground biomass in 2010 for large trees ($> 10 \text{ cm}$) was $63.3 \text{ Mg C ha}^{-1}$ (wet site) and

$65.3 \text{ Mg C ha}^{-1}$ (dry plot). Total stand level biomass for small trees ($< 10 \text{ cm}$) was 2.9 Mg C ha^{-1} (wet) and 3.1 Mg C ha^{-1} (dry). Hence, total stand level above-ground biomass was $66.2 \text{ Mg C ha}^{-1}$ (wet plot) and $68.4 \text{ Mg C ha}^{-1}$ (dry plot), effectively identical at the two sites.

Dividing the above-ground wood biomass by the above-ground wood biomass productivity, we estimated stem biomass residence times of 22 and 26 years for the two plots. The low value of the biomass residence time (most Amazonian sites have reported a value between 50 and 100 years (Galbraith et al. 2013)) suggests that either the plots have very high dynamism, or else that they are not close to equilibrium, probably having suffered a loss in biomass in a past fire disturbance, and are rapidly increasing in biomass following the disturbance.

To estimate the effect of moisture expansion (of bark or xylem) on apparent tree growth during the wet season, we separated the trees with almost no annual tree growth (woody NPP $< 1 \text{ kg C ha}^{-1} \text{ year}^{-1}$) and determined their apparent seasonal trends in diameter. For these slow growing trees we found a mean seasonal amplitude of apparent growth peaking in April and then decreasing until October. We estimated the seasonal effect of moisture expansion between March and November (the maximum and minimum) to be $0.08 \text{ Mg C ha}^{-1} \text{ month}^{-1}$ at Kenia-wet and $0.19 \text{ Mg C ha}^{-1} \text{ month}^{-1}$ at Kenia-dry (although this may underestimate the effect, since faster growing trees tend to shrink more in the dry season, because they possess larger vessels).

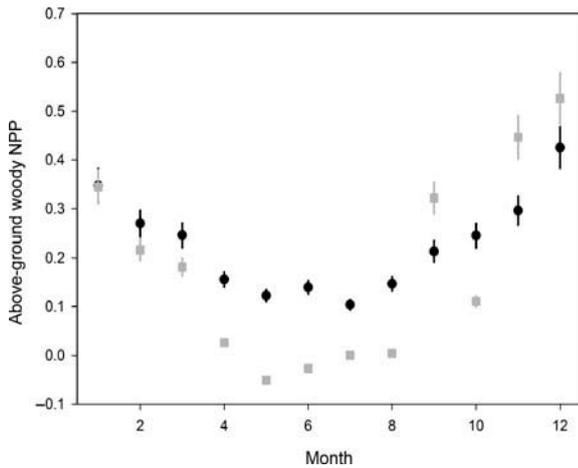


Figure 3. Woody NPP ($\text{Mg C ha}^{-1} \text{ month}^{-1}$) using dendrometer bands, measured every month over a 2-year period for the Kenia-wet (black) and Kenia-dry (grey) plots in the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia. Error bars indicate a measurement error of 10%.

We measured the DBH of all stems >10 cm in 2008, 2009 and 2010, and found that NPP_{ACW} at Kenia-wet was $2.71 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ and NPP_{ACW} at Kenia-dry averaged $2.10 \text{ Mg C ha}^{-1} \text{ year}^{-1}$. We scaled our dendrometer data so that its annual average was equal to our census data, since the census spanned all trees in the plot, and then corrected the seasonal cycle for moisture expansion. Even after this correction, there was a strong seasonality in woody NPP, with a peak in woody growth in January to $0.43 \text{ Mg C ha}^{-1} \text{ month}^{-1}$ and a minimum in August at $0.10 \text{ Mg C ha}^{-1} \text{ month}^{-1}$, a more than fourfold change in growth rate (Figure 3). Kenia-dry showed a similar but more extreme seasonal pattern, with growth peaking in January at $0.53 \text{ Mg C ha}^{-1} \text{ month}^{-1}$ and a minimum in August with essentially no growth ($-0.05 \text{ Mg C ha}^{-1} \text{ month}^{-1}$) (Figure 3). We estimated coarse root NPP as 21% of stem NPP, and therefore $0.57 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for Kenia-wet and $0.44 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for Kenia-dry.

Canopy NPP

Both sites peaked in total litterfall between April and September, with Kenia-wet averaging $0.66 \text{ Mg C ha}^{-1} \text{ month}^{-1}$ at the peak and $0.30 \text{ Mg C ha}^{-1} \text{ month}^{-1}$ during the other months. Kenia-dry averaged $0.49 \text{ Mg C ha}^{-1} \text{ month}^{-1}$ at the peak and $0.22 \text{ Mg C ha}^{-1} \text{ month}^{-1}$ during the other months (Figure 4). Total canopy NPP was $5.65 \pm 0.65 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-wet and $4.23 \pm 0.57 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-dry (Table 4). Of this total, the ratio of leaves, twigs and reproductive litter was 52:13:24 (wet plot) and 53:12:26 (dry plot). Twig fall was notably high at both plots. Of this, leaves accounted for $2.91 \pm 0.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-wet and $2.22 \pm 0.57 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-dry. We attributed the NPP loss rate to herbivory of $0.55 \pm 0.06 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-wet and $0.42 \pm 0.05 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-dry (Table 4).

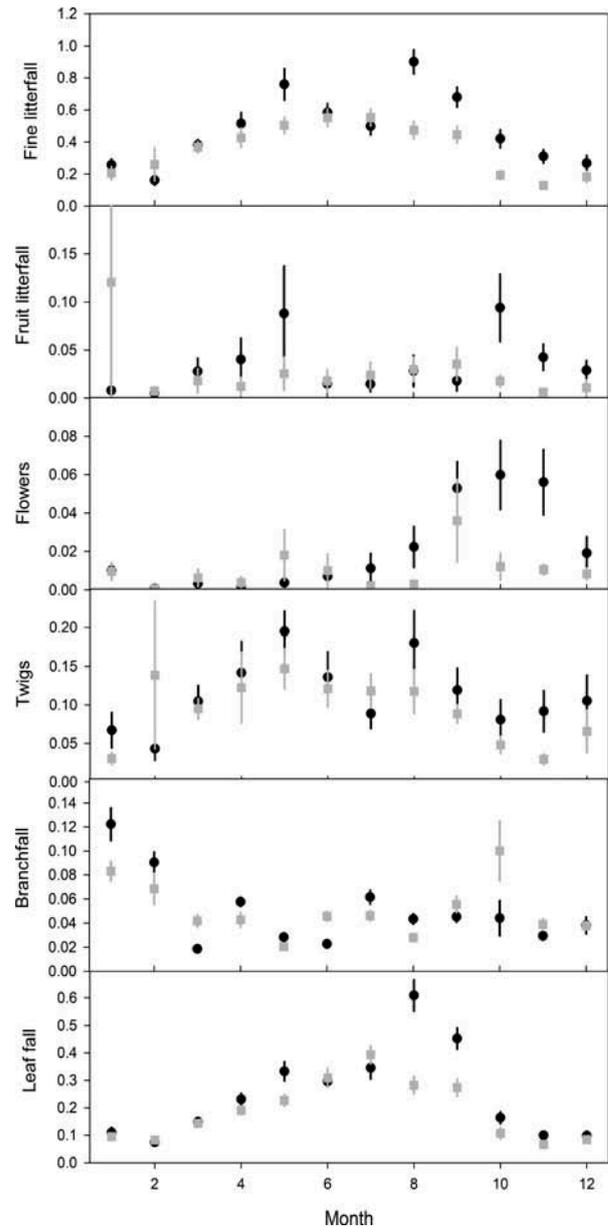


Figure 4. Sum of the monthly collections from 25 litter traps of total litter, fruit, flowers, twig, branch fall, and leaf NPP ($\text{Mg C ha}^{-1} \text{ month}^{-1}$) measured over a 2-year period for the Kenia-wet (grey) and Kenia-dry (black) plots in the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia. Error bars are standard errors.

Branch turnover NPP

Total annual $NPP_{\text{branch turnover}}$ averaged $0.57 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-wet and $0.58 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-dry (Table 4). At both sites there was a strong seasonal cycle, with $NPP_{\text{branch turnover}}$ greatest in January and lowest in June.

Soil respiration

To control for the effect of the mixing of the soil during our partitioning experiment, we compared the effect of a disturbance on the soil cores. Total respiration for the undisturbed

Kenia-wet cores differed by 10%, a non-significant difference ($P > 0.05$). At Kenia-dry, total respiration differed by 4%, also not significantly. Hence we did not need to apply a disturbance correction to the soil respiration partitioning analysis.

We calculated the average percentage respiration attributable to the rhizosphere by subtracting monthly values of tubes, excluding rhizosphere respiration from those including rhizosphere and heterotrophic respiration. Averaged monthly values of root respiration at Kenia-wet were 34% of soil respiration. This varied seasonally, with June to October values averaging 30% and the rest of the year 36%. Averaged monthly root respiration values at Kenia-dry were 23% of soil respiration throughout the year.

Total soil respiration exhibited a significant seasonal cycle ($P < 0.001$) and was lowest between May and September at both sites (Figure 5). Total annually averaged soil respiration was not significantly different between sites and averaged $13.86 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-wet and $12.83 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-dry.

Total rhizosphere respiration showed a significant seasonal cycle ($P < 0.001$), and was lowest between May and September at both sites (Figure 5). Total annually averaged rhizosphere respiration was significantly different between sites ($P < 0.001$) and averaged $4.40 \pm 0.55 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-wet and $2.40 \pm 0.29 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-dry (Table 4).

Total heterotrophic soil respiration also had a significant seasonal cycle ($P < 0.001$) and was again lowest between May and September at both sites (Figure 5). Total annually averaged heterotrophic soil respiration was not

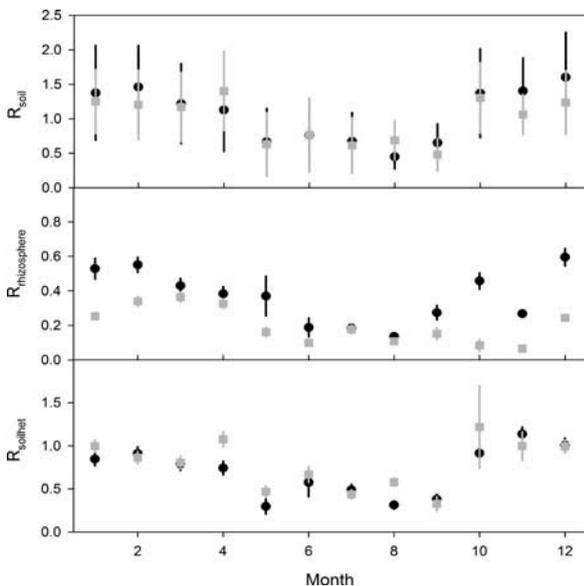


Figure 5. (top) Total soil respiration from 25 permanent locations, (middle) autotrophic respiration ($\text{Mg C ha}^{-1} \text{ month}^{-1}$) and (bottom) heterotrophic respiration ($\text{Mg C ha}^{-1} \text{ month}^{-1}$) measured monthly over a 2-year period for the Kenia-wet (black) and Kenia-dry (grey) plots in the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia. Autotrophic respiration was determined by an exclusion experiment ($N = 16$), where respiration was measured from tubes after roots and mycorrhizae had been removed. Error bars indicate standard errors.

significantly different between sites, and averaged $8.47 \pm 0.98 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-wet and $9.51 \pm 1.37 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-dry.

Wood respiration

The estimated total woody surface area of large trees ($>10 \text{ cm}$ diameter) at Kenia-wet was $11,900 \text{ m}^2 \text{ ha}^{-1}$ and $10,700 \text{ m}^2 \text{ ha}^{-1}$ at Kenia-dry. The total woody surface area of small trees ($<10 \text{ cm}$ diameter) was $541 \text{ m}^2 \text{ ha}^{-1}$ for Kenia-wet and $735 \text{ m}^2 \text{ ha}^{-1}$ for Kenia-dry. We calculate a total stem area index (SAI), the woody surface area per ground area, of $1.24 \text{ m}^2 \text{ m}^{-2}$ for Kenia-wet and $1.15 \text{ m}^2 \text{ m}^{-2}$ for Kenia-dry. Woody respiration was significantly greater at Kenia-wet ($P < 0.05$), averaging $2.19 \pm 0.13 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for all our measurements and $1.99 \pm 0.11 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for Kenia-dry.

To scale these measurements to the plot level we looked for a relationship between woody NPP and woody respiration for these 25 trees. There was a significant positive linear relationship between woody NPP and trunk respiration for both Kenia-wet and Kenia-dry. We scaled these equations to the whole plot and found that the trees measured for woody respiration grew faster than average, and we therefore had to reduce our estimates for respiratory fluxes by about 20% at Kenia-wet and ca. 10% at Kenia-dry when scaled to the entire plot.

We then multiplied the total plot woody surface area by our scaled woody respiration fluxes (Figure 6). There was a significant seasonal cycle in wood respiration at both sites, with respiration peaking in the wet season, being greatest during April (Kenia-wet) and June (Kenia-dry) and least in August. There was no significant difference between the sites when compared on a monthly timescale. Total annual woody respiration at Kenia-wet was estimated to be $7.44 \pm 0.90 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ and $7.26 \pm 0.99 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-dry (Table 4).

Leaf respiration and photosynthesis

Sun leaves had significantly greater dark respiration rates than shade leaves at Kenia-wet. Due to a very open canopy

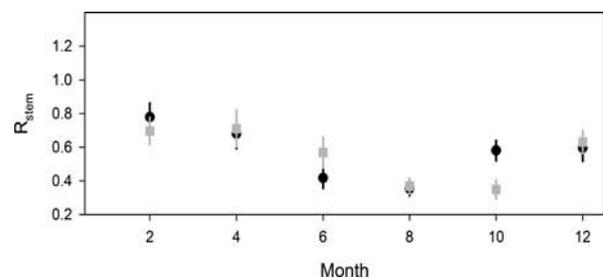


Figure 6. Above-ground wood respiration from collars on 25 trees measured every two months and multiplied by the total woody surface area of the plot ($\text{Mg C ha}^{-1} \text{ month}^{-1}$) measured every two months over a 2-year period for the Kenia-wet (black) and Kenia-dry (grey) plots in the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia. Error bars are standard errors of the mean.

Table 5. Mean (\pm SE) leaf dark respiration (R) in the dry and wet seasons and light-saturated photosynthesis (A) values in the wet season for sun and shade leaves for Kenia-wet and Kenia-dry, Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia. Units are $\mu\text{mol m}^{-2} \text{s}^{-1}$. Asterisks represent significant differences ($P < 0.05$) between the plots.

	R Dry Sun	R Dry Shade	R Wet Sun	R Wet Shade	A Wet Sun	A Wet Shade
Kenia-wet	0.83 ± 0.08	0.66 ± 0.08	0.80 ± 0.08	0.65 ± 0.09	$6.0 \pm 0.98^*$	5.3 ± 0.90
Kenia-dry	0.92 ± 0.07	no shade	0.63 ± 0.07	no shade	3.1 ± 0.67	no shade

there were no shade leaves at Kenia-dry. There were no significant differences in dark leaf respiration between the wet and dry season at Kenia-wet, but there was a significant increase in leaf respiration during the dry season at Kenia-dry (Table 5).

In June, light-saturated sunlit leaf photosynthesis was significantly greater ($P < 0.05$) at Kenia-wet ($6.0 \pm 0.98 \mu\text{mol m}^{-2} \text{s}^{-1}$) than at Kenia-dry ($3.1 \pm 0.67 \mu\text{mol m}^{-2} \text{s}^{-1}$). In November, light-saturated sunlit leaf photosynthesis was significantly greater ($P < 0.05$) at Kenia-wet ($2.92 \pm 0.85 \mu\text{mol m}^{-2} \text{s}^{-1}$) than at Kenia-dry ($-0.29 \pm 0.09 \mu\text{mol m}^{-2} \text{s}^{-1}$). The entire forest at Kenia-dry appeared to have little carbon uptake due to the extended drought in 2010. A_{max} was significantly lower in November than in June at both Kenia-wet and Kenia-dry.

At Kenia-wet LAI averaged $2.80 \pm 0.17 \text{ m}^2 \text{ m}^{-2}$, 2.33 ± 0.12 between July and October, and $3.07 \pm 0.19 \text{ m}^2 \text{ m}^{-2}$ over the rest of the year. LAI averaged $2.20 \pm 0.14 \text{ m}^2 \text{ m}^{-2}$ at Kenia-dry, $1.49 \pm 0.13 \text{ m}^2 \text{ m}^{-2}$ between July and October and $2.64 \pm 0.14 \text{ m}^2 \text{ m}^{-2}$ the rest of the year. Because Kenia-dry was deciduous and lost almost all its leaves in the dry season, we were able to verify our estimates with litterfall and specific leaf area (SLA). Since average litterfall at Kenia-dry was 9.74 g m^{-2} , we estimated an average LAI of $1.75 \text{ m}^2 \text{ m}^{-2}$, which was close to but slightly lower than our LAI estimate of $2.20 \text{ m}^2 \text{ m}^{-2}$, made from hemispherical photos, implying that we may have been overestimating canopy respiration at the plot level. The difference probably arose since at low LAI values optical methods tend to overestimate LAI by including components of stem and branch area. With full deciduousness, the true LAI at Kenia-dry in the dry season is close to zero.

When scaled up to the whole canopy there was little seasonality in our estimate of leaf respiration, nor did we find a significant relationship between trunk NPP and dark leaf respiration. To account for light inhibition of dark respiration, we multiplied our result by 0.67 (as in Malhi et al. 2009). Total annual canopy respiration averaged $5.23 \pm 0.55 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-wet and $4.43 \pm 0.35 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at Kenia-dry.

We calculated leaf flush at both sites by adding our leaf fall figure to the monthly change in leaf area index (as in Doughty and Goulden 2008). We found a bimodal peak in leaf flushing at Kenia-wet, with peaks in March and September (Figure 7). These results approximately match our observations of leaf flush from the site.

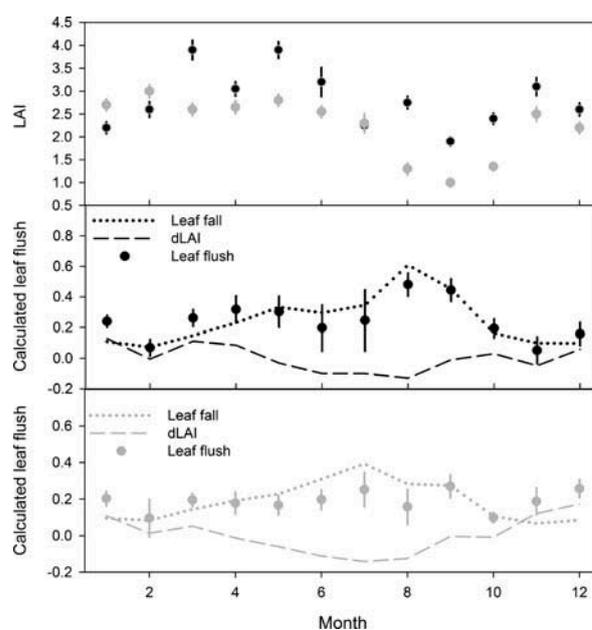


Figure 7. (top) Leaf area index (LAI) ($\text{m}^2 \text{ m}^{-2}$) based on 25 hemispherical photographs taken every month over a two-year period. Calculated leaf flush ($\text{Mg C ha}^{-1} \text{ month}^{-1}$) (solid line) using LAI (dashed line) and leaf fall (dotted line) for the Kenia-wet (middle) and Kenia-dry (bottom) plots in the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia. Error bars indicate the standard error across the 25 measurement points in each plot.

Total productivity, autotrophic respiration and CUE

We added annually averaged fine root NPP, above-ground woody NPP, branch NPP, canopy NPP, herbivory and estimated coarse root NPP (21% of above-ground woody NPP) to estimate a plot level NPP of $15.50 \pm 0.89 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for Kenia-wet and $11.27 \pm 0.68 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for Kenia-dry (Figure 8). We added annually averaged rhizosphere respiration, woody respiration and leaf respiration to estimate total autotrophic respiration at $18.64 \pm 2.78 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for Kenia-wet and $15.61 \pm 2.61 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for Kenia-dry. We added total autotrophic respiration to total heterotrophic respiration to give an estimate of total GPP at $34.14 \pm 2.92 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for Kenia-wet and $26.88 \pm 2.70 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for Kenia-dry. We divided total NPP from total GPP to estimate carbon use efficiency (CUE) at 0.45 ± 0.05 at Kenia-wet and 0.42 ± 0.05 at Kenia-dry (Table 4).

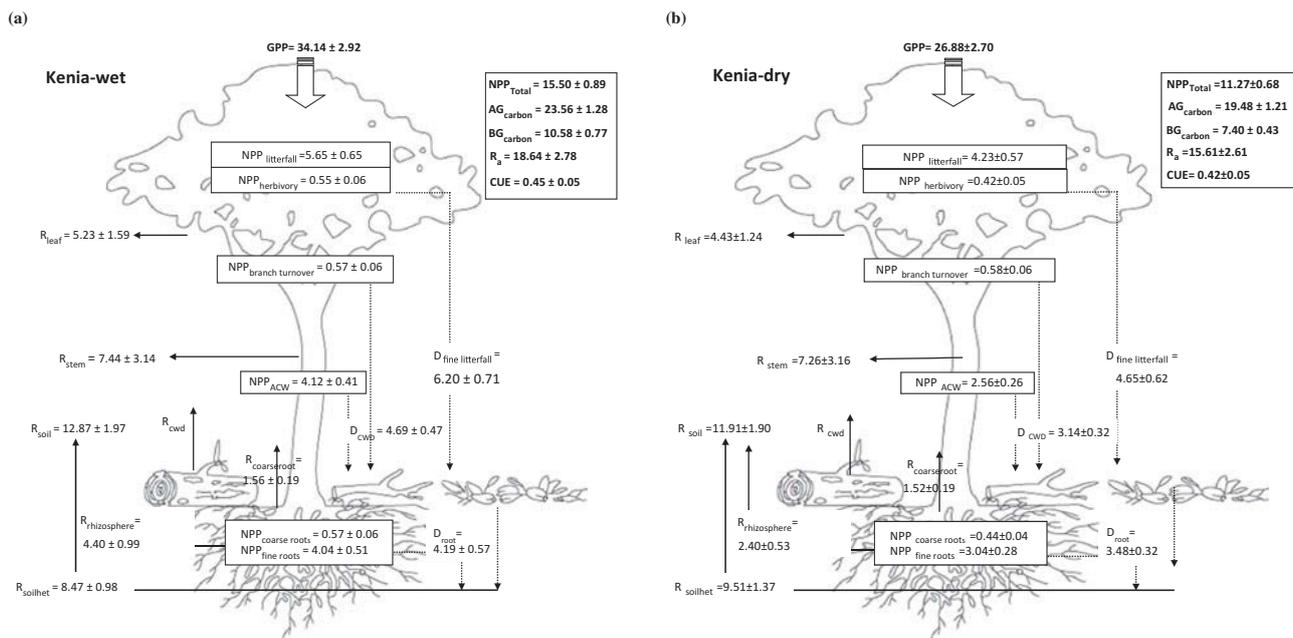


Figure 8. Diagram showing the magnitude and pattern of key carbon fluxes for the Kenia-wet (a) and Kenia-dry (b) plots in the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia. Components with prefixes R , NPP and D denote respiration, net primary productivity and decomposition terms respectively. Detailed descriptions of C flux components measured are presented in Tables 2 and 3. All values are in units of $\text{Mg C ha}^{-1} \text{ year}^{-1}$, with the exception of carbon use efficiency (CUE) which is calculated as total NPP/GPP . GPP , gross primary productivity; R_a , autotrophic respiration; R_h , heterotrophic respiration. Errors include sample error caused by spatial heterogeneity of the measured parameter within the study plots (standard error of the mean), together with an estimate of uncertainties due to measurement/equipment biases and scaling up localised measurements to the plot level.

Discussion

The two plots had a very different species composition, with Kenia-dry having many drought-deciduous tree species, while Kenia-wet had species more typical of lowland evergreen rainforest. Despite these very large species level differences, there were in fact few large edaphic or climatic differences between the two plots. The soils on both sites had similar physical characteristics and relatively high nutrient concentrations (Table 1). Since the sites were only ca. 2 km from one another they had similar climate, temperature and rainfall patterns. The main difference appeared to be in the soil drainage properties, with differences in the depth of the bedrock (ca. 1 m at Kenia-dry and >2 m at Kenia-wet), and the sloped topography at Kenia-dry which enhanced drainage, resulting in drier soil.

These differences in drainage properties led to relatively small but nonetheless significant differences in average 0–18 cm soil moisture content between the two plots. However, due to the shallow bedrock in Kenia-dry, the total available water is probably much lower. The measured soil moisture was at the lower end of the values observed for tropical forests. The total annual rainfall was $1352 \text{ mm year}^{-1}$ for both plots, which put our sites towards the low end of precipitation for Amazonian forests (Malhi et al. 2009).

Could the difference in species composition be due to a prior disturbance event, such as a fire or a drought? Fires are common in the area and both sites had been burned around five years prior to the start of the study. More

likely, however, was the possibility of a major drought, since these occur in the region (Lewis et al. 2011) and occasionally accentuate the existing differences in soil water to the degree that drought-deciduous tree species would gain a survival edge at the drier plot.

Kenia-dry had lower LAI (Figure 7) and lower average leaf photosynthesis than Kenia-wet (Table 5). The abundant drought-deciduous trees in Kenia-dry lost most of their leaves in the dry season (Figure 7), further decreasing total photosynthesis. This led to the largest difference in carbon cycling between the two plots: the large difference in total photosynthesis with GPP much lower at Kenia-dry ($26.88 \text{ MgC ha}^{-1} \text{ year}^{-1}$) than at Kenia-wet ($34.14 \text{ MgC ha}^{-1} \text{ year}^{-1}$). We estimate that the difference in total GPP of ca. $7 \text{ MgC ha}^{-1} \text{ year}^{-1}$ was mainly due to the lower LAI and leaf photosynthesis in the drought-deciduous tree species. Remarkably, the wetter site had GPP similar to that observed in wet humid forests in Brazil, despite the much lower rainfall (Malhi et al. 2009b). Hence, it appears that strong seasonal drought does not present much of a constraint on photosynthesis in evergreen forests (e.g. through stomatal closure), and annual GPP only reduces substantially when drought-deciduous species begin to dominate the canopy.

We might expect the carbon use efficiency to differ between Kenia-wet and Kenia-dry, with greater investment in leaf, stem and fine root maintenance throughout the dry season in Kenia-wet. However, despite the large differences in species composition and GPP , the two plots had similar

CUEs. At both plots, CUE was high (0.45 at Kenia-wet and 0.42 at Kenia-dry), typical of a forest that has been recovering from disturbance (DeLucia et al. 2007; Malhi et al. 2009b). These plots may still be recovering from the major fire in the region that burned both plots in 2004, allocating a larger percentage of their carbon gain towards growth versus respiration. Alternatively, the estimated high stem dynamism of this plot may result in the forest having an equilibrium state that involves high amounts of tree-level disturbance. Evidence is emerging that the dry margin of the humid Amazon forest biome may be characterised by naturally high turnover rates, irrespective of disturbance rates (Rocha et al., 2014).

NPP allocation was remarkably similar between the two plots, despite the very different seasonality of the leaf canopies. Tropical forests typically allocate $34 \pm 6\%$ of NPP to canopy, $39 \pm 10\%$ to wood production and $27 \pm 11\%$ to fine roots (Malhi et al. 2011). We found broadly similar patterns at both plots, with slightly more NPP allocated to the canopy than average and slightly less to wood (Table 6). It should be noted that our study included NPP components (such as herbivory and branch turnover) which were not addressed in the estimates by Malhi et al. (2011). Once these are taken into account the allocation patterns are close to the mean for tropical forests. Despite large differences in species composition, allocation patterns were similar, in terms of NPP allocation and Kenia-dry acted as a scaled-down, less productive version of Kenia-wet.

We also measured the seasonality of different carbon cycling components. There was significant seasonality in all the carbon cycling measurements, as well as in the autotrophic respiration. We expected a strong seasonality in the drier deciduous forest, but found almost as much seasonality at Kenia-wet. Seasonality of fine root NPP coincided with that of woody NPP, with both peaking in the wet season and being at a minimum in the dry season. The combination of decreased precipitation and decreased

solar radiation in June–July may strongly decrease photosynthesis during these periods and contribute to the strong seasonality apparent at both sites.

The evergreen Kenia-wet plot displays strong seasonality in leaf flush with a bimodal peak in March and October. This suggests that new leaves are flushing to coincide with the peaks in radiation in advance of the rainy season and the austral winter. This has similarities to sites in the eastern Amazon, where leaf flush tends to correspond with the dry season, when there is most sunlight (Doughty and Goulden 2008).

There were large absolute differences between the two plots in most of the carbon cycling components in Kenia-wet and Kenia-dry. However, these differences were directly proportional to the total NPP and GPP, and hence the allocation of photosynthate was very similar between the two plots. It is initially surprising that the two very different plots in terms of forests composition had similar carbon allocation patterns. Why would a dry deciduous-type forest not allocate more carbon towards roots and a wet-type forest not allocate more carbon towards leaves? Perhaps, these forests that straddle the wet/dry forest ecotone, both at their range limit, revert to the most conservative allocation pattern that enables them to maximise height, water uptake and photosynthesis. For instance, because Kenia-wet is at the dry limit that humid species can exist, there is no additional carbon to allocate to one particular component, such as leaves. Likewise, to avoid being outcompeted by the more productive humid species, the dry deciduous species could not allocate more carbon towards roots at the expense of carbon for tree height or leaves.

If this region dries in the future, we might expect the drought-deciduous species such as those in Kenia-dry to outcompete the humid species, as has been seen in Ghanaian forests during an increased dry period (Fauset et al. 2012). This may lead to forests in this region that are less productive and have lower total NPP and GPP, but with similar biomass and carbon allocation patterns.

Table 6. Patterns of carbon allocation, NPP allocation, and partitioning of autotrophic respiration in Kenia-wet and Kenia-dry, our two study plots in the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia. BG is below-ground and AG is above-ground.

	Kenia-wet		Kenia-dry	
	Mean	SE	Mean	SE
Total carbon allocation				
AG carbon ($\text{Mg C ha}^{-1} \text{ year}^{-1}$)	23.56	1.28	19.48	1.21
BG carbon ($\text{Mg C ha}^{-1} \text{ year}^{-1}$)	10.58	0.77	7.40	0.43
AG fraction (%)	0.69	0.04	0.72	0.05
BG fraction (%)	0.31	0.02	0.28	0.02
Allocation of NPP				
Canopy (%)	0.40	0.07	0.41	0.08
Wood (%)	0.34	0.02	0.32	0.02
Fine roots (%)	0.26	0.03	0.27	0.03
Partitioning of autotrophic respiration				
Canopy (%)	0.28	0.03	0.28	0.02
Wood (%)	0.48	0.05	0.56	0.06
Rhizosphere (%)	0.24	0.03	0.15	0.02

Conclusions

Our two plots represent forest types in the transition zone between the humid forest, represented by Kenia-wet, and the dry forest that borders it, represented by Kenia-dry. The two plots had very different forest structure and floristic characteristics. This difference appears to be driven by differences in soil moisture resulting from differing soil drainage characteristics. The decreased soil moisture at Kenia-dry encouraged the growth of drought-deciduous trees with lower photosynthesis and lower total GPP. CUE and NPP allocation patterns were similar between the plots, suggesting that in terms of carbon allocation the dry forests of the southern Amazon act as a scaled-down version of the wetter humid forests. The low tree biomass and stature, and the high CUE and NPP, may be a response to the 2004 fire, but more probably characterise the structure and dynamic characteristics typical of the dry margin of the Amazon forest biome.

Acknowledgements

This study is a product of the Amazon Forest Inventory Network (RAINFOR) consortium and the Global Ecosystems Monitoring (GEM) network, and was funded by a grant from the Gordon and Betty Moore Foundation.

We thank R. Castedo (owner), R. Melgar (logistic coordinator), P. Tomicha (foreman) and J. Surubi (cowboy) of the Hacienda Kenia. We also thank D.E. Guari of the Hacienda Jorochito and the Museo Noel Kempff Mercado for logistical support for the research.

YM was supported by the Jackson Foundation and the Oxford Martin School.

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