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Spatial and temporal variation of forest net primary productivity components on contrasting soils in northwestern Amazon

Eliana M. Jiménez [1,2,†] María Cristina Peñuela-Mora [3] Flavio Moreno [4] and Carlos A. Sierra [2]

[1]*Instituto Amazónico de Investigaciones IMANI, Universidad Nacional de Colombia Sede Amazonia, Km. 2 vía Tarapacá, Leticia, Colombia*
[2]*Max Planck Institute for Biogeochemistry, P.O. Box 10 01 64, Jena 07701 Germany*
[3]*Grupo de Ecosistemas Tropicales y Cambio Global, Universidad Regional Amazónica-Ikiam, Ciudad de Tena, Napo, Ecuador*
[4]*Departamento de Ciencias Forestales, Facultad de Ciencias Agrarias, Universidad Nacional de Colombia Sede Medellín, Medellin, Colombia*

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Abstract. Climate is a strong determinant of tropical forest productivity; therefore, it is often assumed that Amazonian forest growing on the same local rainfall regime responds similarly to fluctuations in rainfall, independently of soil differences among them. We evaluated intra- and inter-annual variation of net primary productivity (NPP) components, and forest dynamics during 2004–2012 yr in five forests on clay, clay-loam, sandy-clay-loam, sandy-loam and loamy-sand soils, and the same local rainfall regime in northwestern Amazonia (Colombia). The questions were as follows: (1) Do NPP components and forest dynamics respond synchronously to temporal rainfall fluctuations? (2) Are the responses between above and belowground components and forest dynamics similar for different forest stands? A slight and complex synchronicity among different NPP components in their response to temporal rainfall fluctuations were found; few plots showed that aboveground biomass (AGB) and stem growth were susceptible to rainfall fluctuations, while belowground components (fine roots) showed correlation with one-month lagged rainfall. Furthermore, despite that northwestern Amazonia is considered relatively aseasonal, litterfall showed high seasonality in the loam-soil forest group, as well as the fine-root mass, particularly during the 2005 drought. Litterfall correlation with rainfall of sandy-loam terra-firme forest was time lagged as well as fine-root mass of the loamy-sand forest. The correlation between mortality and rainfall was weak, except for the loamy-sand forest (white-sand forest, 77%). High mortality rates occurred in the non-flooded forests for the censuses that included the dry years (2004–2005, 2005–2006). Interestingly, litterfall, AGB increment, and recruitment showed high correlation among forests, particularly within the loam-soil forest group. Nonetheless, leaf area index (LAI) measured in the most contrasting forests (clay and loamy-sand soil) was poorly correlated with rainfall, but highly correlated among them, which could be indicating a phenotypic response to the incident radiation in these sites; also, LAI did not reflect the differences in NPP components and their response to rainfall. Overall, the different temporal behavior of NPP components among forests in relation to rainfall fluctuations suggests the important role that soil exerts on the responses of plant species in each site, besides their effect on forest dynamics and community composition.

Key words: aboveground productivity; carbon allocation; Colombian Amazon; leaf area index; net primary production; white-sand forests.

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† **E-mail:** emjimenez@unal.edu.co

Introduction

Carbon dynamics in forest ecosystems are highly susceptible to weather extremes, with tree mortality and carbon allocation components (biomass and fluxes) being strongly affected by such events (Reichstein et al. 2013). Among the different climatic factors affecting the carbon balance of tropical lowland rainforests, drought has received the most attention (Corlett 2011, Allen et al. 2015) and is considered as the most widespread factor (Reichstein et al. 2013, McDowell et al. 2018). The effect of droughts on Amazon forests has been of particular concern due to its role in the global carbon cycle (Meir et al. 2009, Meir and Woodward 2010, Davidson et al. 2012, Zhou et al. 2013). According to Davidson et al. (2012), the susceptibility of the Amazon basin to drought likely varies regionally, depending on local climate (total rainfall and its seasonal distribution), and soil water storage properties (soil texture and depth) to which the existing vegetation is physiologically adapted. Moreover, drought experiments (Nepstad et al. 2002, 2007, Brando et al. 2008, da Costa et al. 2010) and permanent plots (Williamson et al. 2001, Phillips et al. 2009, 2010, Lewis et al. 2011) have shown high mortality and substantial decreases in carbon allocation to aboveground components (biomass [AGB] and net primary production [NPP]) due to drought events; however, trends of belowground components are less clear (Brando et al. 2008).

Most of our current understanding of forest responses to rainfall comes from basin-wide analyses of satellite-derived indices or forest plots (Phillips et al. 2009, 2010, Lewis et al. 2011, McDowell et al. 2018). A myriad of studies investigating the response of Amazon forests to drought have yield diverging and contrasting results (Saleska et al. 2007, Malhi et al. 2009, Phillips et al. 2009, Brando et al. 2010, Lewis et al. 2011, Rammig et al. 2010, Samanta et al. 2012, Saatchi et al. 2013). Although some of these discrepancies may be explained by differences among methodological approaches between studies, several have found important differences in drought between forests with marked dry seasons in the east and southeast of the Amazon Basin, and the less-seasonal forests in the northwestern region (Brando et al. 2008, Meir et al. 2009, da Costa et al. 2010). For instance, local variability imposed by differences in soil structure and community composition could be responsible for the diverging results (Quesada et al. 2012, Quesada and Lloyd 2016*a*, *b*). So far, there is a paucity of studies conducted on contrasting soils investigating intra- and inter-annual fluctuations in processes such as mortality, recruitment, and the partitioning of NPP components (leaf, stem, and root growth), and how they respond to temporal rainfall variability.

In this study, we evaluated the intra- and inter-annual variation of NPP components and forest dynamics of five forest types in western Amazonia growing under the same local climate regime on different soils. We examined whether these forests respond similarly to rainfall fluctuations as suggested by model projections, given that our plots fall within a single grid point of a regional simulation. To that end, we investigated the following research questions: (1) Do NPP components and forest dynamics respond synchronously to temporal rainfall fluctuations? (2) Are the responses between above and belowground components and forest dynamics similar for five old-growth forests growing on different soils? It is important to notice that the severe droughts of 2005 and 2010 are included in our eight-year period of observation, which should be crucial for understanding drought effects on the forest carbon balance in the Amazon basin.

Methods

Site description

This research was conducted in the northwestern Amazon basin (Colombia), in five mature forests on soils of different origin and texture. Two 1-ha plots were located at the Amacayacu National Natural Park (AGP plots) and four plots at the Zafire Biological Station (ZAR plots; Table 1).

The study sites are approximately 50 km apart and experience similar climatic conditions, typical of a perhumid lowland equatorial climate. Annual rainfall ranges from 2561 to 3902, with an average of 3351 mm/yr (±323 mm/yr), according to data for 1973–2012 from the meteorological station at the Vásquez Cobo airport in Leticia (04°11′36″ S; 69°56′35″ W). The monthly mean rainfall for this period was

Table 1. Description of study sites in the northwestern Amazon (Colombia): Amacayacu National Natural Park (AGP) and Zafire Biological Station (ZAR).

Forest type†	Plot code	Soil classification‡	Coordinates	Altitude (m)	$[P]_a$	[N]	CEC	Stem density	Basal area
Clay-soil forest group									
Clay-soil terra-firme	AGP-01	Endostagnic Plinthosol (Alumic, Hyperdystric)	3.72 S; 70.31 W	105	25.36	0.15	6.21	625	27.75
	AGP-02	Endostagnic Plinthosol (Alumic, Hyperdystric)	3.72 S; 70.30 W	110	25.43	0.16	6.26	574	27.78
Loam-soil forest group									
Loamy-sand terra-firme	ZAR-01	Ortsteinc Podzol (Oxyaquic)	4.01 S; 69.91 W	130	14.36	0.11	0.71	873	16.87
Clay-loam black-water seasonally flooded	ZAR-02	Haplic Gleysol (Alumic, Hyperdystric)	4.00 S; 69.90 W	120	23.16	0.16	3.51	624	26.16
Sandy-clay-loam terra-firme	ZAR-03	Haplic Cambisol (Alumic, Hyperdystric, Clayic)	3.99 S; 69.90 W	135	16.22	0.21	1.93	685	28.78
Sandy-loam terra-firme	ZAR-04	Haplic Alisol (Alumic, Hyperdystric)	4.01 S; 69.90 W	120	8.6	0.10	2.60	658	27.82

Note: Altitude, in m; $[P]_a$, available phosphorus in mg/kg; [N], nitrogen as a percentage; CEC, effective cation exchange capacity in $cmol_c/kg$; stem density, individuals with DBH ≥10 cm in no./ha; basal area in m^2/ha.

† Forest type based on soil texture differences (USDA Classification).

‡ World Reference Base soil classification system, more details of plot soils in Quesada et al. (2010, 2011).

279 mm (±75 mm), and in most years, there is no dry season (defined as rainfall <100 mm/month; Malhi et al. 2004). Although in 2005 there was a marked dry season from June to September with a rainfall between 52 and 98 mm, which was not registered in the last 39 yr (rainfall anomaly calculated as the monthly mean minus the monthly multiannual mean for 1973–2012, presented in Fig. 1). This drought also affected most of the Amazon Basin (Zeng et al. 2008). Mean annual temperature was 26°C (min 24°C, max 27°C) with little variation among seasons and years. Mean annual relative humidity was 86%.

The six 1-ha permanent plots were established in five different forests with contrasting soils (Fig. 2, Table 1). Plots are in decreasing order along a clay content gradient, as follows: (1) clay-soil: AGP-01 and AGP-02 plots, (2) clay-loam: ZAR-02 plot, (3) sandy-clay-loam: ZAR-03 plot, (4) sandy-loam: ZAR-04 plot, and (5) loamy-sand: ZAR-01 plot, all of them described in detail in Quesada et al. (2010, 2011). In general, these clay soils have higher concentrations of available phosphorus (P_a), nitrogen (N), and especially a higher effective cation exchange capacity compared to the loam-soil forest group (ZAR plots on Table 1). Plots also show drainage differences as follow: Four plots are non-flooded upland vegetation called terra-firme; one is located on a floodplain of black water known as igapó (ZAR-02), and the loamy-sand plot (hydromorphic Podzol, ZAR-01) which contains a hardpan at approximately 1-m depth that causes periodic water stagnation in the layers above it (Sierra et al. 2013).

These forests show differences in composition and physiognomy. The upland vegetation or terra-firme forests exhibit more structural and floristic similarities among them than with the black-water seasonally flooded forest or the loamy-sand terra-firme forest. The clay-loam black-water flooded forest (igapó) represents a specialized ecosystem, which is distinct from white-water floodplains (várzea) and the terra-firme forests (Parolin et al. 2004). The loamy-sand forest is known as white-sand forest (Fine et al. 2010, Adeney et al. 2016) or white-sand campinarana (Rossetti et al. 2018), a particular ecosystem dominated by species that only grow on this specific soil type, with shorter trees and lower basal areas.

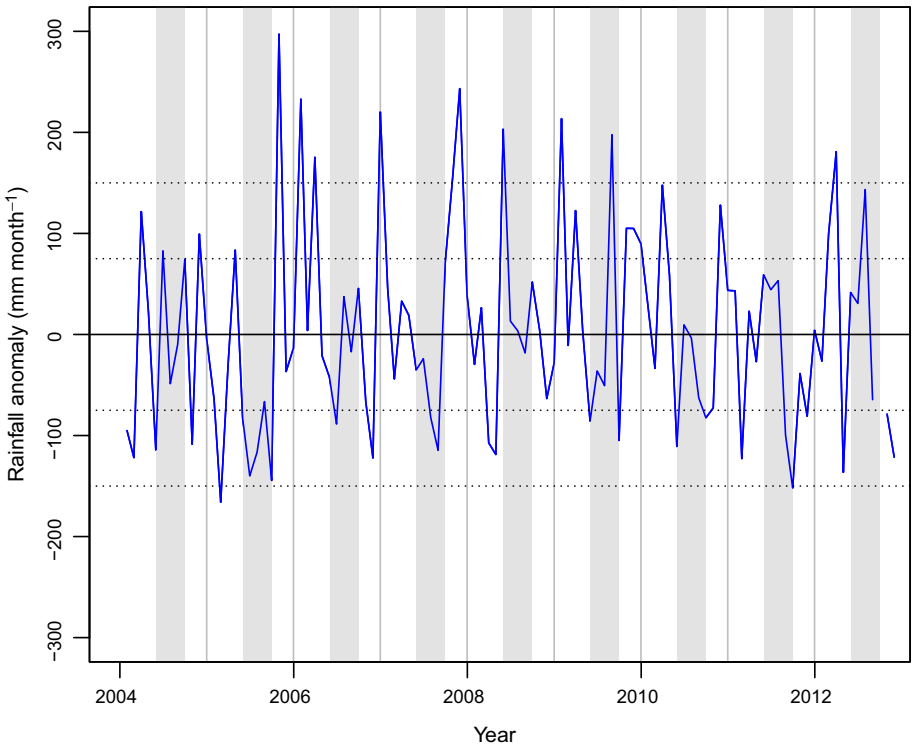

Fig. 1. Rainfall anomaly (mm per month) for the study sites in the northwestern Amazon (Colombia), for 2004–2012 from the meteorological station at the Vásquez Cobo airport in Leticia (04°11′36″ S; 69°56′35″ W). Anomaly rainfall calculated as the observed minus the multiannual average for 1973–2012. The horizontal dotted lines indicate one and two standard deviations, and the shade areas represent the period from June to September of each year, which corresponds to the multiannual dry season, including the dry season of 2005 (with rainfall <100 mm/month).

Intra-annual variation of above and belowground components

We assessed intra-annual variation or seasonality among plots of above and belowground NPP components by making detailed measurements of fine litterfall, stem growth, fine-root mass, and leaf area index (LAI), with methods described in Jiménez et al. (2014). Fine litterfall (leaves, flowers, fruits, and twigs with diameter ≤2 mm and indeterminate material for 2004–2006) was collected bi-weekly, from 25 mesh traps (0.5 m^2) per plot. We calculated the litterfall anomaly as the difference between the observed and the mean litterfall of the monitoring time. Intra-annual measurements were done every three or four months from 2004 to 2006. Stem growth was monitored using dendrometer bands installed on 90% of stems with diameter ≥10 cm (*d* at 1.3 m or above buttresses). The dendrometer bands were settled before making the first measurement with an adjustment period of six months; the increment was registered using a caliper. We measured LAI and fine-root mass in the most contrasting forests: the clay-soil forest (AGP-01 and AGP-02 plots) and the loamy-sand forest (ZAR-01 plot). Leaf area index was estimated indirectly using hemispherical photographs and analyzed with the Hemiview Canopy Analysis Software (version 2.1 SR1; Delta-T Devices, Cambridge, UK); photographs were taken at the same points (26 per plot) during each sampling date (every three–four months) in order to register dry and wet months. Fine-root mass (root diameter ≤2 mm) and its change over time were obtained from soil samples taken monthly at 0.2-m depth using the sequential root coring method (Vogt et al. 1998), and taking the average of fine-root

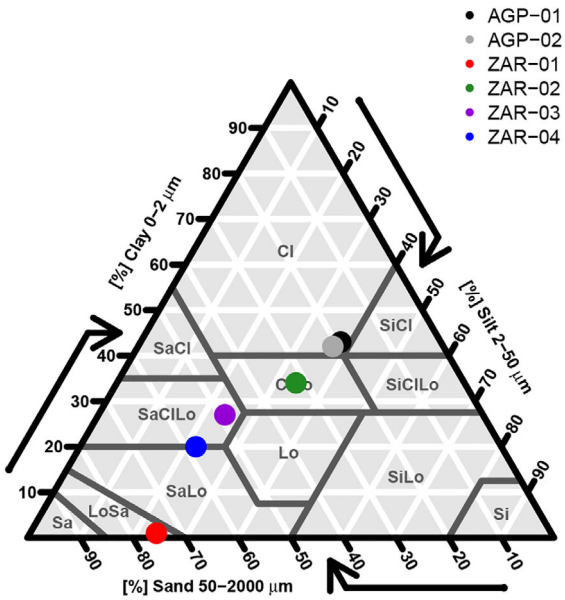

Fig. 2. Soil texture classification for the forest plots of this study, adapted from Soil Textural Triangle of USDA Classification (Thien 1979): (1) Clay-soil terra-firme forests (Cl, AGP-01 and AGP-02 plots); (2) clay-loam black-water seasonally flooded forest (ClLo, ZAR-02); (3) sandy-clay-loam terra-firme forest (SaClLo, ZAR-03); (4) sandy-loam terra-firme forest (SaLo, ZAR-04); and (5) loamy-sand terra-firme forest (LoSa, ZAR-01).

mass for each monitoring period (for details, see Jimenez et al. 2009).

Inter-annual variation of aboveground biomass increment and forest dynamics

We evaluated the inter-annual variation of aboveground biomass (AGB) increment and forest dynamics in the loam-soil forest group at the Zafire Biological Station (ZAR plots in Table 1). Aboveground biomass and NPP were monitored between 2004 and 2012. Aboveground biomass was calculated from stem diameter measurements of all trees and palms with $d \geq 10$ cm. We estimated AGB tree level using a set of allometric equations and report uncertainty due to the choice of allometric model (details in Jiménez et al. 2014). Aboveground biomass was then calculated as the median of biomass estimates from different allometric models.

Aboveground biomass increment was calculated as the increments of surviving trees or palms (difference between the estimated biomass at the beginning of the interval and the end of the interval) plus increments of ingrowth, viz. the difference between its estimated biomass at the end of the interval and the minimum d measured (10 cm; Clark et al. 2001). To convert from dry organic matter to carbon, we assumed a factor of 50%.

Forest dynamics was assessed as mortality and recruitment rates (calculated following Nepstad et al. 2007). During the censuses, dead trees or palms were confirmed and registered in four death categories (Gale and Barfod 1999): standing dead, snapped, uprooted, and missed (disappeared stems previously tagged). We also registered the ingrowth of new individuals that grew during the interval between the censuses and reached d minimum (10 cm).

Error propagation and statistical analysis

We estimated uncertainties in estimated AGB and production through error propagation (details in Jiménez et al. 2014). We considered the uncertainty associated with the biomass estimates from allometric models selected and the spatial variation within the plots (Chave et al. 2004). Briefly, standard errors were calculated as the square of the median absolute deviation divided by the square of the sample size depending on the component analyzed. Errors were propagated as the sum or average of the squared standard errors, depending on the operations performed on the means.

The trend analysis (stationary/non-stationary) and the seasonal decomposition of the series were performed with the StatR and PlotsR applications of the RWizard software (Guisande et al. 2014), and all calculations and statistical tests were performed in the R package (R Development Core and Team 2016) and the scripts described in the books by Guisande et al. (2006, 2011) and Guisande and Vaamonde (2012). The augmented Dickey–Fuller test (ADF, Dickey and Fuller 1979), which removes all the structural effects (autocorrelation) in the time series, was used to determine whether a series is stationary; this test was performed with the function adf.test of the package R tseries (Trapletti and Hornik 2019).

We used Akaike information criterion (AIC) to define whether rainfall affects litterfall in the five forests. The Akaike's method evaluates the goodness of the model by setting a penalty

because of their complexity, so a simpler model is preferable to another with additional independent variables that explain only a small additional portion of the variability of the dependent variable. In general, AIC = $2k - 2\ln(L)$, where k is the number of explanatory variables or parameters of the model and L the likelihood or probability associated with the sample used in accordance with the model, so that AIC decreases as the lower the number of variables and the greater the likelihood; among alternative models, the one with the lowest value of AIC must be chosen (Guisande et al. 2011). Therefore, the criterion to determine whether rainfall affects litterfall is to compare the AIC values obtained in the models of litterfall with rainfall included as independent variable and without it (Guisande et al. 2011).

The function auto-arima of the R package forecast (Hyndman and Khandakar 2008, Hyndman et al. 2019) was used to obtain the model with the optimal combination of the autoregressive (p), integration (d), and moving average (q) components, which minimizes AIC for each time series. Due to that rainfall data were monthly, time series with monthly data of litterfall and rainfall were used in the estimation of the models. Finally, the seasonal plots were depicted using the function seasonplot of the R package forecast (Hyndman and Khandakar 2008, Hyndman et al. 2019).

Other intra- and inter-annual correlations of the rest of above and belowground NPP components among forests were tested through a correlation matrix for stem growth, AGB increment, LAI, and fine-root mass, and for forest dynamics a correlation matrix for mortality and recruitment rates. In addition, we evaluated the correlation between rainfall and every component or rate. We evaluated the correlation of NPP components and forest dynamic rates with the current rainfall registered during the measurements. Additionally, using a cross-correlation test, we evaluated the correlation of fine-root mass with time lags of rainfall.

Results

Intra-annual variation of above and belowground components

Litterfall production.—All the P values obtained from the augmented Dickey–Fuller test applied to the time series of litterfall in five forest types of Amazon were higher than 0.05 (Table 2). Therefore, the null hypothesis that the time series is stationary is accepted as much as there is not significant trend in any of the time series.

Temporal behavior of litterfall was clearly different among the five Amazon forests evaluated (Fig. 3). There was not a clear seasonal pattern in the clay-soil forest, because there was no season of the year with higher values of litterfall. Meanwhile, in the loam-soil forest group, litterfall was higher in August–September, with a smaller peak in April–May, so the seasonal pattern was more pronounced.

Furthermore, the clay-soil forest plots exhibited a very different intra-annual variation pattern compared to the loam-soil forest group. Litterfall decreased in the clay-soil forest plots during the dry season of 2005, followed by a spike thereafter. On the contrary, litterfall in the loam-soil forests group showed an increase in the transition between the dry and the wet season, highlighted in 2005.

In almost all models obtained with the auto.-arima function, the components p, d, and q were zero (Table 3). The autoregressive component (p) shows the portion of the value of the variable that depends on the values above in the history of the series; that is, a zero value means that the present values are not affected by previous months; therefore, only in ZAR-04, where $p = 1$, the present month is affected by the previous one. The integration component (d) indicates whether the times series is stationary. As all d values were zero, the time series are stationaries, in agreement with the results obtained from the augmented Dickey–Fuller

Table 2. Probabilities obtained from applying the augmented Dickey–Fuller test to the time series of litterfall in each forest type.

Forest type	Plot code	*P*
Clay-soil forest group		
Clay-soil forest	AGP-01	0.973
	AGP-02	0.963
Loam-soil forest group		
Loamy-sand forest	ZAR-01	0.844
Clay-loam flooded forest	ZAR-02	0.426
Sandy-clay-loam forest	ZAR-03	0.498
Sandy-loam forest	ZAR-04	0.523

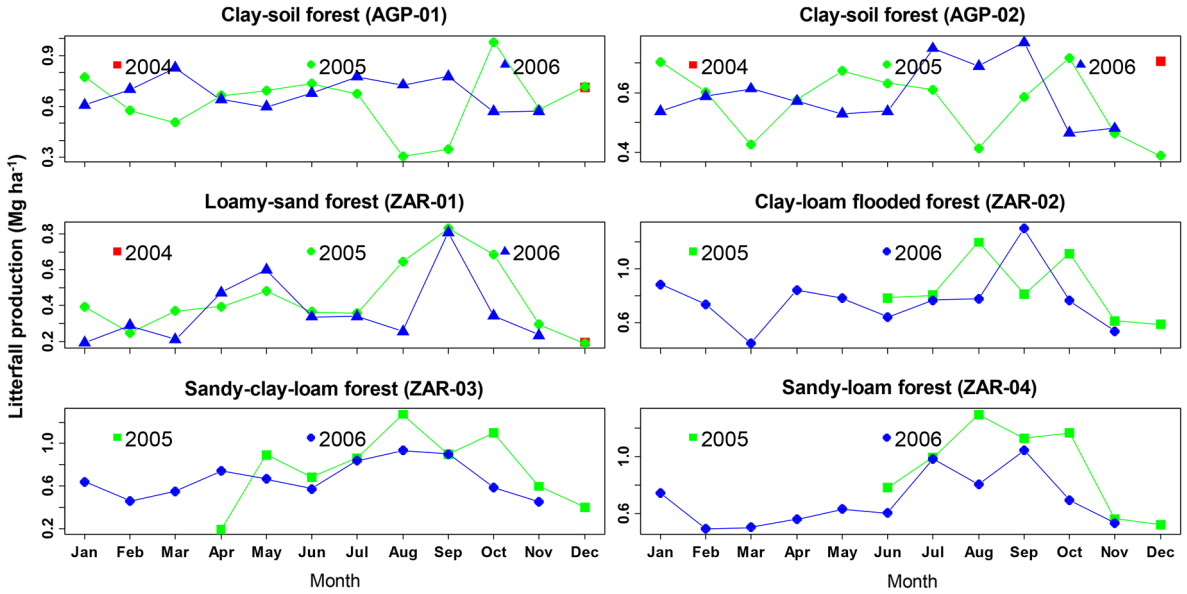

Fig. 3. Seasonal litterfall variation of five Amazon forests. The measurements were done from October 2005 to December 2006.

Table 3. Values obtained from the function auto.arima of the autoregressive component (p), integration component (d), component of moving average (q) for the non-seasonal and seasonal components, and the AIC, with and without rainfall as independent variable, for each of the five Amazon forests.

			Non-seasonal components			Seasonal components			
Forest type	Plot code	Rainfall	p	d	q	p	d	q	AIC
Clay-soil forest	AGP-01	No	0	0	0	0	0	0	−22.1
		Yes	0	0	0	0	0	0	−25.5
	AGP-02	No	0	0	0	0	0	0	−35.3
		Yes	0	0	0	0	0	0	−35.0
Loamy-sand forest	ZAR-01	No	0	0	0	0	0	0	−8.1
		Yes	0	0	0	0	0	0	−7.3
Clay-loam flooded forest	ZAR-02	No	0	0	0	0	0	0	−0.6
		Yes	0	0	0	0	0	0	1.4
Sandy-clay-loam forest	ZAR-03	No	0	0	0	0	0	0	5.1
		Yes	0	0	0	0	0	0	5.6
Sandy-loam forest	ZAR-04	No	1	0	0	0	0	0	1.5
		Yes	1	0	0	0	0	0	−0.04

Note: AIC, Akaike information criterion.

test. The component of moving average (q) shows whether there is any external variable affecting the time series. As all q values were 0, it means that there is not innovation in the series, so the time series are mainly explained by the inertia or the previous or the historical behavior. Finally, the AIC values comparing the model with and without rainfall seem to corroborate that the time series were not affected by rainfall in most of the forests, because the values were very similar between both models. The exception was the clay-soil (AGP-01) and the sandy-loam (ZAR-04) forests, whose AIC values were slightly lower in the model with

Table 4. Correlation matrices of litterfall production and stem growth of individuals among different Amazon forest plots.

Net primary component	Plot code	Clay-soil forest		Loamy-sand forest	Clay-loam flooded forest	Sandy-clay-loam forest	Sandy-loam forest
		AGP-01	AGP-02	ZAR-01	ZAR-02	ZAR-03	ZAR-04
Litterfall production	AGP-01	1					
	AGP-02	0.5448**	1				
	ZAR-01	−0.2252	0.1502	1			
	ZAR-02	−0.0553	0.3352	0.7386***	1		
	ZAR-03	−0.1433	0.2714	0.6730***	0.7858***	1	
	ZAR-04	−0.1743	0.3072	0.7061***	0.7814***	0.9174***	1
Stem growth of individuals	AGP-01	1					
	AGP-02	0.8855**	1				
	ZAR-01	0.2976	0.4087	1			
	ZAR-02	−0.6784	−0.3425	0.4192	1		
	ZAR-03	−0.5935	−0.5301	0.5885	0.7754*	1	...

Note: Missing data of stem growth of individuals for sandy-loam forest (ZAR-04) due to very small measurement periods not suitable for calculation of correlation coefficients.
* $P \leq 0.1$, ** $P < 0.05$, *** $P < 0.01$.

rainfall, indicating that litterfall was somewhat affected by rainfall in these two Amazon forests.

Finally, litterfall was significantly correlated among the plots in the loam-soil group (Table 4), as well as between the two clay-soil forest plots (correlation coefficient of 54%), but there were not correlations among the plots between the two soil groups.

Stem growth.—Stem growth showed seasonality (Fig. 4) and was highly correlated with rainfall in some of the loam-soil plots (Table 5). In the clay-loam black-water flooded and the sandy-clay-loam forests, stem growth was highly correlated with rainfall (97% and 82%, respectively). Contrary to litterfall production, stem growth was poorly correlated among forest types (Table 4). The strongest correlation among forests was between plots with high clay content, particularly between the clay-soil plots AGP-01 and AGP-02 (88%), and between the clay-loam black-water flooded forest and the sandy-clay-loam forest (78%).

Leaf area index.—Leaf area index was significantly correlated among the clay-soil forest and the loamy-sand forest plots (white-sand forest; Fig. 5, Table 6). Overall, the magnitude of the correlation with rainfall was low (Table 5), and there were differences between plots within the same forest type. For instance, despite that plots on clay soils are considered the same forest type (and are located only 300 m apart), one plot on clay soil exhibited a negative correlation with rainfall ($\rho = -0.34$, $P = 0.1$) while the other showed a very low positive and not significant correlation with it ($\rho = 0.06$).

Fine-root mass.—Fine-root mass from the two most contrasting soils (clay and loamy-sands) did not show a significant correlation with the current rainfall; nevertheless, fine-root mass from one plot of the clay-soil forest and the loamy-sand forest showed correlation with one-month lagged rainfall (Fig. 6). Furthermore, temporal trends in fine-root mass showed differences among forests (Fig. 5). The loamy-sand forest displayed the highest values of fine-root mass at the start of the dry season, particularly marked in 2005, while the clay-soil forest plots exhibited the highest values at the start of the wet season (December 2005). The correlation of fine-root mass between forest plots (Table 6) was significant between the clay-soil forest plots (72%); however, it was uncorrelated between them and the loamy-sand forests.

Inter-annual variability

Aboveground biomass increment.—In the loam-soil forests group (ZAR plots), AGB biomass increment showed significant correlation with rainfall in forests containing high clay content: clay-loam flooded forest and sandy-clay-loam forest, with 88% and 76%, respectively (Table 5). These forests displayed the lowest values of AGB increment for the periods of lower rainfall

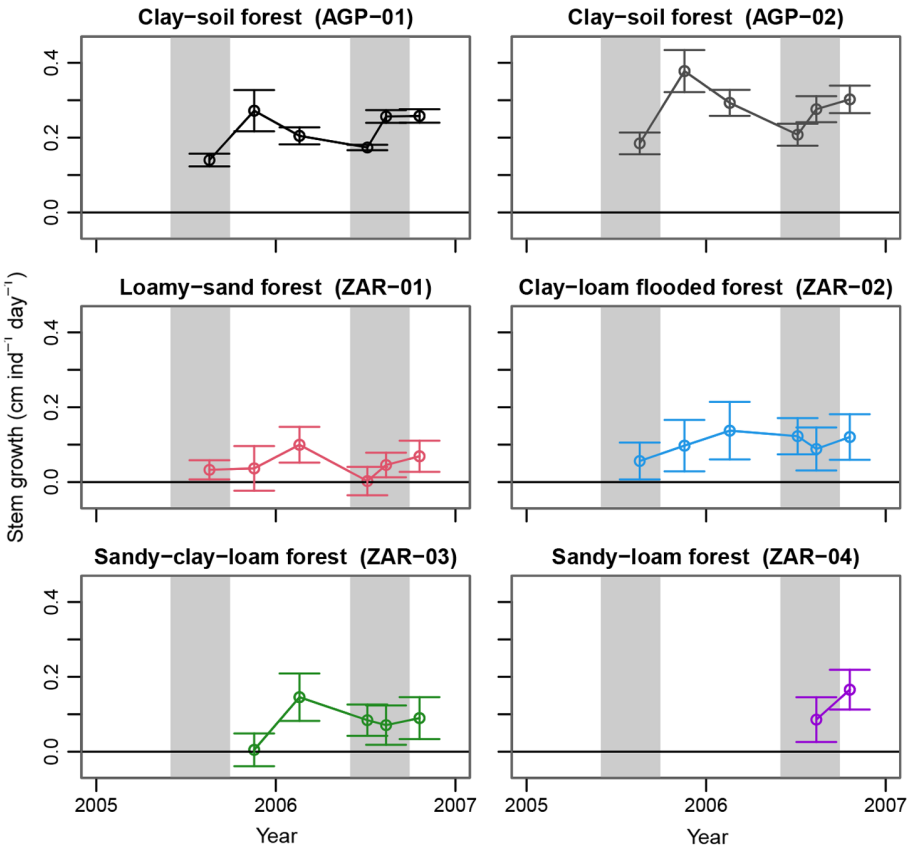

Fig. 4. Stem growth measured with dendrometer bands in individuals of the different Amazon forest plots for 2005 and 2006. The shade areas represent periods where the driest months can occur, including the dry season of 2005 (June–September with rainfall <100 mm/month).

Table 5. Correlation coefficients of above and belowground NPP components, forest dynamics, and LAI of Amazon forests with rainfall.†

Forest type	Plot code	Aboveground NPP		LAI	Belowground NPP	Forest dynamic rates	
		Stem growth	AGB increment		Fine-root mass	Mortality	Recruitment
Clay-soil forest	AGP-01	−0.3818	...	0.0562	−0.3804	...	...
	AGP-02	−0.1373	...	−0.3427*	−0.0512	...	...
Loamy-sand forest	ZAR-01	0.5853	0.3277	0.0342	−0.2867	0.7673*	0.1777
Clay-loam flooded forest	ZAR-02	0.9651***	0.8787**	...	...	−0.0532	−0.0525
Sandy-clay-loam forest	ZAR-03	0.8221*	0.7582*	...	...	0.1972	−0.0607
Sandy-loam forest	ZAR-04	...	−0.1819	...	...	0.5230	0.2096

Note: LAI, leaf area index; NPP, net primary productivity. Missing data correspond to unavailable measurements for some plots or very small measurement periods not suitable for calculation of correlation coefficients.

† The correlation with rainfall was stem growth, LAI, and fine-root mass with the rainfall of three or four months, aboveground biomass (AGB) increment, and forest dynamic rates with annual rainfall. Litterfall component was evaluated in Tables 2, 3.

*$P \leq 0.1$, **$P < 0.05$, ***$P < 0.01$.

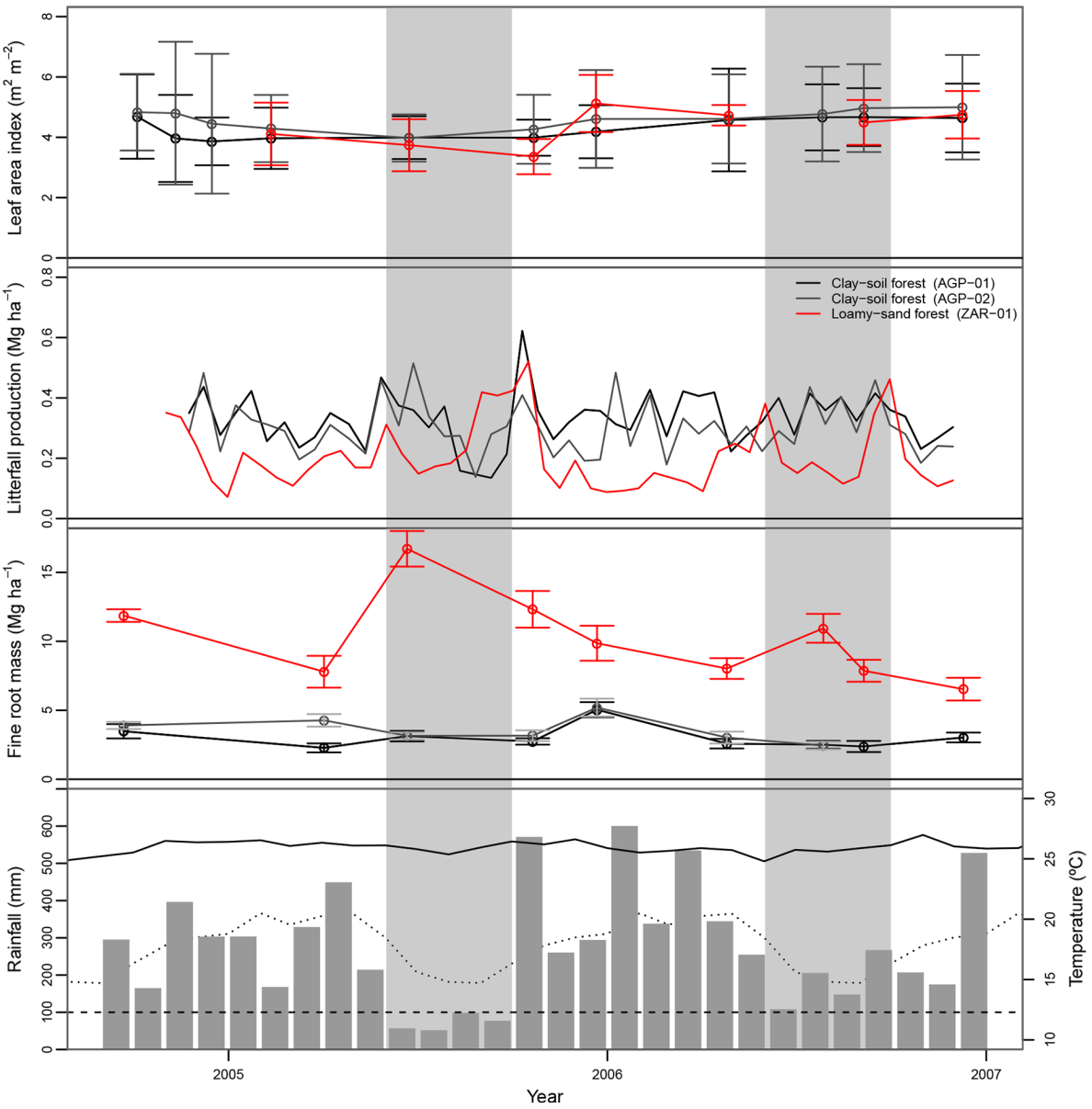

Fig. 5. Intra-annual variation of leaf area index, litterfall production, and fine-root mass of two forests on contrasting soils in the Amazon Basin. The shade areas represent periods where the driest months can occur, including the dry season of 2005 (June–September with rainfall <100 mm/month).

(Fig. 7), including the driest years of 2005 and 2011. The sandy-loam forest, with a low correlation with rainfall, showed the lower values of AGB increment both in dry (2004–2005 and 2009–20012) and wet years (2006–2007 and 2007–2008; Fig. 7).

The AGB increment was highly correlated among forests with similar basal area (Table 1), with correlation coefficients varying from 88% to 92% (Table 7); clay-soil forest plots had similar basal area but they were not included in this analysis because there was not enough data to evaluate it.

Forest dynamics.—Annual mortality and recruitment rates were highly variable among forests and over the years (Fig. 8). Overall, these

Table 6. Correlation matrix of leaf area index and fine-root mass between two Amazon forests on contrasting soils.

Net primary component	Plot code	Clay-soil forest		Loamy-sand forest
		AGP-01	AGP-02	ZAR-01
Leaf area index	AGP-01	1		
	AGP-02	0.8996***	1	
	ZAR-01	0.6374*	0.7061*	1
Fine-root mass	AGP-01	1		
	AGP-02	0.7235*	1	
	ZAR-01	0.1868	−0.3007	1

*$P \leq 0.1$, **$P < 0.05$, ***$P < 0.01$.

variables were poorly correlated with rainfall (Table 5); only mortality rates of the loamy-sand forest (ZAR-01) exhibited a positive correlation with rainfall ($\rho = 0.77$, $P < 0.1$), which displayed the highest mortality rates in the periods 2005–2006 and 2009–2012 (1.7% and 2.8%, respectively; Fig. 1).

Correlations among forests were significant for recruitment rates, but not for mortality rates (Table 5). The high and significant correlation of the recruitment rates among forests is a trend observed over the years (Fig. 8); the forests exhibited the highest recruitment rates between 2008 and 2009, varying from 1% to 3.6% for the sandy-loam and the loamy-sand forests, respectively, whereas low rates were more variable over time. With regard to mortality rates, the most correlated forests were the sandy-clay-loam and the sandy-loam forests (coefficient of 70%), as well as the sandy-clay-loam and the loamy-sand forests (correlation coefficient of 66%; $P = 0.15$). Overall, excluding the clay-loam flooded forest, mortality mostly occurred during drought events in 2005–2006 and in the period 2009–2012 (Fig. 8). Finally, the proportion of death stems by category for these dry years in the same non-flooded forests with high mortality rates, the most important type of death was the standing type for the 2004–2005 and 2005–2006 censuses (Fig. 9).

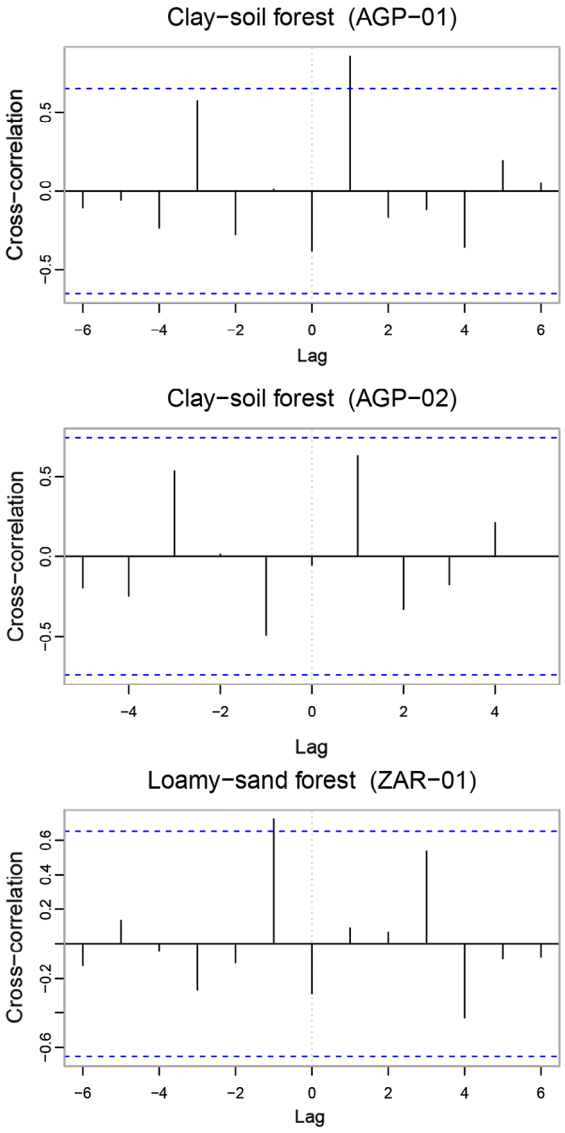

Fig. 6. Correlation between fine-root mass and rainfall with different lags (months). Cross-correlation above the dotted lines indicates significant correlation.

Discussion

Responses of NPP components to rainfall

Despite the studied forest stands are growing under similar climatic conditions in terms of amount and seasonal distribution of solar irradiance and rainfall, their NPP components exhibited spatial and temporal differences in response to fluctuations in rainfall. Consequently, the correlation of above and below-ground NPP components with rainfall showed high variation among forest types, which suggests that soils play an important role in the responses of forests to rainfall fluctuations. Hofhansl et al. (2014) also found that NPP components were affected by local topography (water

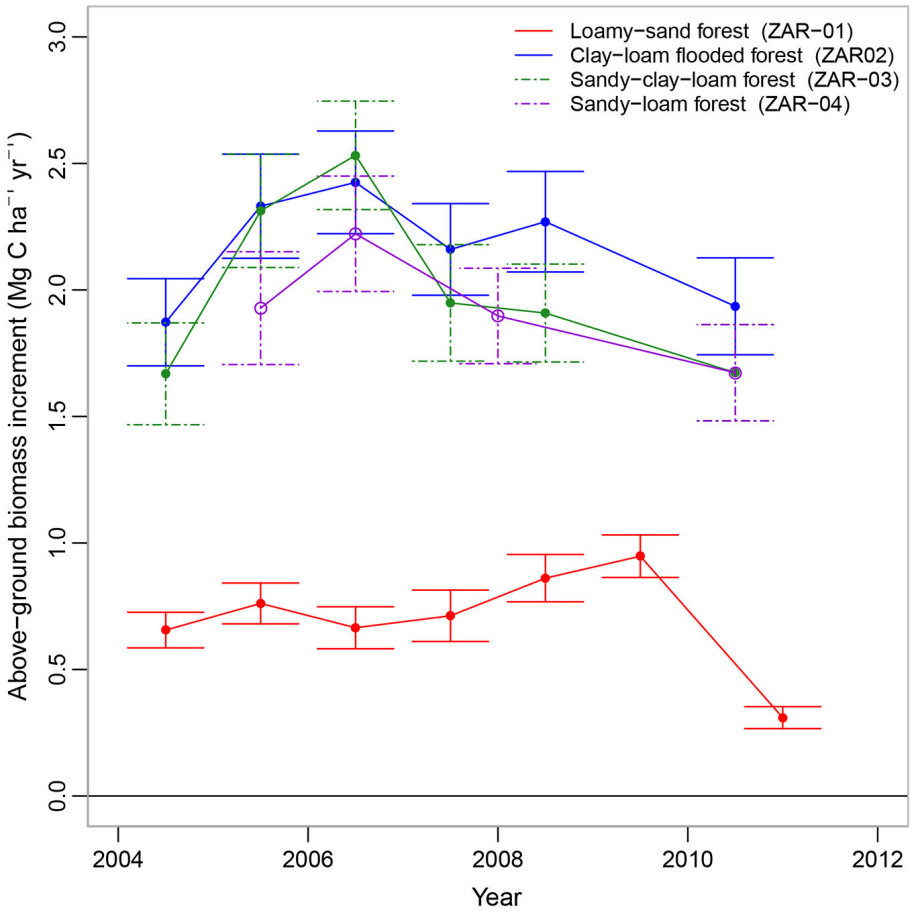

Fig. 7. Aboveground biomass increment for different Amazon forest plots. Points represent the median, and lines the mean standard deviation.

availability) in forests of Costa Rica; they concluded that the impact of climate anomalies on tropical forest productivity is strongly related to local site characteristics and therefore will likely prevent uniform responses of tropical lowland forests to projected global changes. It has been suggested that soil properties related to water storage capacity (mainly texture and depth) are important for determining the susceptibility of Amazon forests to drought events (Davidson et al. 2012); such events could affect plant physiology, phenology, and carbon allocation patterns (Reichstein et al. 2013).

Litterfall seasonality has been reported significantly and positively correlated with rainfall (Chave et al. 2010, Girardin et al. 2014). However, contrary to the expectations derived from these results, litterfall showed important differences among the forests studied (Fig. 3). For example, although the clay-soil forest did not show a clear seasonal pattern and both plots showed the same behavior, there were differences between years and litterfall rates decreased during the dry season of 2005, while the loam-soil forests group showed an increase. Fine-root mass showed high seasonality in the loam-soil forests group (similarly to litterfall), particularly during the 2005 drought.

The inter-annual variability of AGB increment also suggests notable differences in forest responses to both dry and wet years (Fig. 7). Although the lowest rates of AGB increment in most forests coincided with the driest years (2005 and 2011), the loamy-sand forest also displayed a

Table 7. Correlation matrices of aboveground biomass increment, the annual mortality, and recruitment rates among different Amazon forest plots (loam-soil forest group, ZAR plots on Table 1).

Net primary or forest dynamic component	Forest type	Plot code	Loamy-sand forest ZAR-01	Clay-loam flooded forest ZAR-02	Sandy-clay-loam forest ZAR-03	Sandy-loam forest ZAR-04
Aboveground biomass increment	Loamy-sand forest	ZAR-01	1			
	Clay-loam flooded forest	ZAR-02	0.5604	1		
	Sandy-clay-loam forest	ZAR-03	0.2673	0.9153***	1	
	Sandy-loam forest	ZAR-04	0.3850	0.9243*	0.8794*	1
Mortality rates	Loamy-sand forest	ZAR-01	1			
	Clay-loam flooded forest	ZAR-02	−0.0164	1		
	Sandy-clay-loam forest	ZAR-03	0.6619	−0.2589	1	
	Sandy-loam forest	ZAR-04	0.5565	−0.2242	0.7045	1
Recruitment rates	Loamy-sand forest	ZAR-01	1			
	Clay-loam flooded forest	ZAR-02	0.8463**	1		
	Sandy-clay-loam forest	ZAR-03	0.6772*	0.8813*	1	
	Sandy-loam forest	ZAR-04	0.8992*	0.9012*	0.8912*	1

*$P \leq 0.1$, **$P < 0.05$, ***$P < 0.01$.

low AGB increment during 2006–2007, registered as very wet years. This result could be consequence of waterlogged soils during the wet season due to the hardpan, which highlights the importance of assessing variable spatial responses to extreme events. Nevertheless, for all forests, AGB increment augmented after periods of low wood production, indicating that forests recovered rapidly from drought or flooding events, which has also been reported in other tropical forests (Hofhansl et al. 2014). Drought experiments in Amazon forests have shown that wood production is the most affected component of NPP by the exclusion of rainfall or changes in soil moisture availability (Brando et al. 2008, da Costa et al. 2010); litterfall responses were less clear and diverged from the responses of stem growth or aboveground coarse wood production. In summary, results show that under drought events, the forests responded asynchronously allocating carbon to a specific forest component (e.g., fine-root production in sandy forest or litterfall or wood growth in clay forest).

Contrary to NPP components, LAI did not display strong correlation with rainfall in these forests. This suggests that LAI did not reflect the responses of aboveground NPP components (litterfall, stem growth, and AGB increment) to fluctuations in rainfall. Brando et al. (2008) found that LAI declined in response to drought with little effect on litterfall under experimental conditions; we also found a decline in LAI for the 2005 drought in the loamy-sand forest; however, this forest also showed high litterfall production during the same period. Our LAI and litterfall data for the 2005 drought did not show the greenness trend proposed for some parts of the Amazon Basin (Saleska et al. 2007), suggesting that the role of LAI as an indirect measure of changes in aboveground production or canopy greenness should be taken cautiously. Our data also confirm that results from remote-sensing approaches need to be corroborated comprehensively with ground data before drawing general conclusions (Samanta et al. 2012, Chave et al. 2019).

Responses of forest dynamics to rainfall

Overall, recruitment and mortality rates showed little susceptibility to rainfall in these forests. Mortality rates were significantly correlated with rainfall only in the loamy-sand forest (ZAR-01). This forest showed the highest mortality rates during the 2005–2006 and 2009–2012 censuses (Fig. 8), periods that included the marked droughts of 2005 and 2011 (Fig. 1). The non-flooded forests also exhibited high annual mortality rates in the 2005–2006 censuses, as expected from the major drought that affected most of the Amazon Basin (Phillips et al. 2009). Likewise, in the 2010 basin-wide drought (Lewis et al. 2011, Potter et al. 2011), the loamy-sand (ZAR-01), sandy-clay-loam (ZAR-03), and sandy-loam forests (ZAR-04) exhibited high

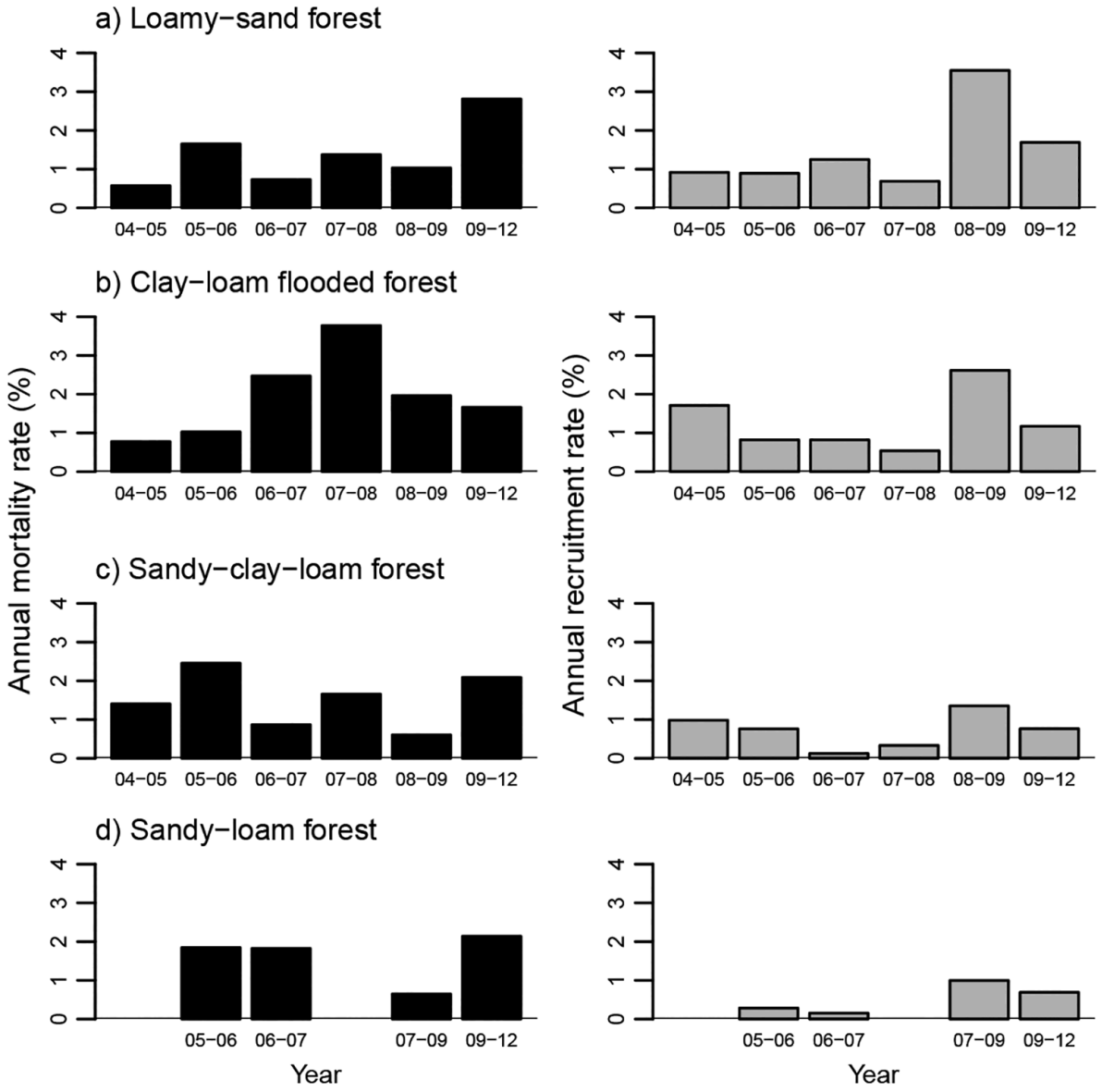

Fig. 8. Annual mortality and recruitment rates of Amazon forests (loam-soil forest group on Table 1), for 2004–2012 yr.

mortality rates, except the clay-loam flooded forest (ZAR-02); the last one also showed the lowest annual mortality rates in drought years of 2004–2005 and 2005–2006 censuses (Fig. 8).

According to drought experiments, Amazon forests can show high mortality rates caused by rainfall exclusion (Nepstad et al. 2007, Brando et al. 2008, da Costa et al. 2010); however, we do not know with certainty the natural range of variability of mortality (Davidson et al. 2012), which hinders the evaluation of the extent to which recent extreme droughts affected tree mortality rates. Death type proportions for each forest (Fig. 9) showed that standing death is the most common death type registered, particularly in the terra-firme forests. This result suggests the occurrence of cavitation (Rowland et al. 2015) and therefore possible physiological failures

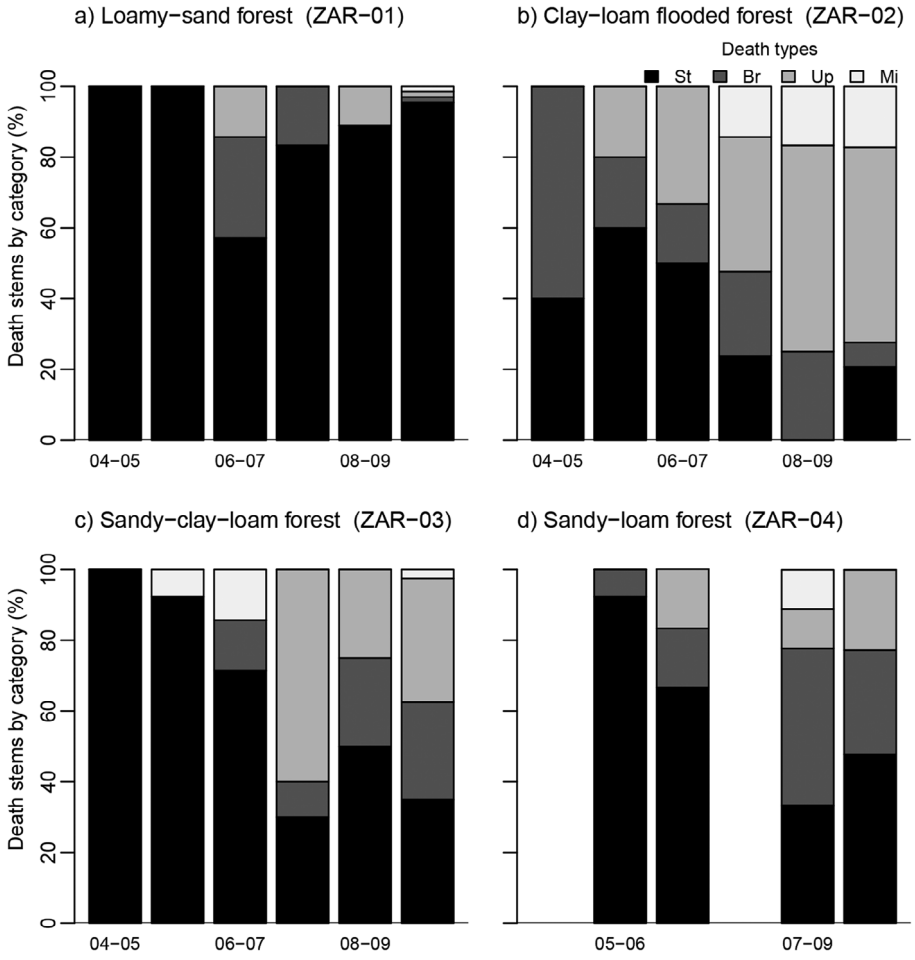

Fig. 9. Proportion of deaths as recorded in field measurements: standing death (St), broken top (Br), uprooted (Up), or missed (Mi) from inventory. Data for four forests 1-ha plots in the loam-soil forest group (Table 1), for 2004–2012 yr.

related to drought at least for the non-flooded forests.

The variability of the stem and biomass increments over the years and among forests suggests an important impact of mortality on them (Figs. 4, 7). This has also been shown in throughfall experiments (Brando et al. 2008, da Costa et al. 2010) and from permanent plots (Phillips et al. 2009). Accordingly, in addition to annual rainfall, other factors might be affecting mortality and recruitment rates, suggesting that forests with different soil properties could also respond in different ways to extreme events, which can affect growth and the net uptake of carbon regionally. It has been documented that forests with different soil properties might differ in stand structure and species composition and therefore respond differently to drought events (Engelbrecht et al. 2007, Quesada et al. 2012, Quesada and Lloyd 2016); this means that not only soil water availability but also functional responses of species growing in sites of varying soil properties could play a role in the observed effects of climate variation on forests.

Variation of NPP components and dynamics among forests

Temporal variation of NPP components was highly correlated between clay-soil forests, but not among them and the loam-soil forest group

(ZAR plots). Also, correlations among plots of the last group were more variable; for example, they were high between all plots for litterfall, while for stem growth correlations were significant only between plots ZAR-02 and ZAR-03; likewise, for biomass increment the plot ZAR-01 did not significantly correlate with any other plot of the group, as expected given its particular soil and vegetation. The low correlation for the temporal variation of NPP components between the clay-soil forests and the loam-soil forests gives additional evidence on the different behavior of these processes influenced by soil properties. Furthermore, the less synchrony of NPP components among plots within the loam-soil forest group (i.e., among plots with less homogeneous soils) strongly supports the hypothesis of the intense effect of soils in controlling carbon allocation in these forests.

Leaf area index was also significantly correlated, not only between the clay-soil forest plots, but also between each of these plots and the loamy-sand forest, the most contrasting forest in terms of soil texture and vegetation structure, suggesting that LAI did not reflect differences in NPP and carbon allocation processes between forest types. This result is remarkable because most of our current understanding of forest responses to rainfall comes from basin-wide analyses of satellite-derived indices or forest plots (Phillips et al. 2009, 2010, Lewis et al. 2011). However, the fidelity of time series of LAI, the fraction of absorbed photosynthetically active radiation, or the enhanced vegetation index and their means of extrapolation remain highly controversial (Nemani et al. 2003, Saleska et al. 2007, Samanta et al. 2010, 2011, Zhao and Running 2010, Medlyn 2011). However, despite these uncertainties, LAI is generally used to calculate NPP in many ecosystem models (Malhi et al. 2011), even though the relationship between satellite-based indices of seasonal greenness and ecosystem productivity remains as an unsolved debate (Davidson et al. 2012).

Studies based on basin-wide analyses of forest dynamics have shown the importance of mortality in AGB change and its possible impacts on the global carbon balance (Phillips et al. 2009), considering that mortality affects the mean residence time of carbon and consequently its stocks in the ecosystem (Brienen et al. 2015). Although the observed lack of correlation of mortality both with rainfall and among forests in the present study could be due to the relatively small sample size, it might indicate that climate is not the only factor inducing mortality in tropical forests (McDowell et al. 2018).

Gathering data across larger spatial scales and at higher temporal resolution should result in more conclusive analyses in order to better understand the tropical forest ecosystem functioning under future scenarios of climate change.

Conclusions

Five forests from the northwestern Amazon basin on different soils and with differences in forest structure, but growing on the same local climatic conditions, showed differential above and belowground carbon allocation responses to rainfall and its seasonality.

Based on measurements from the 2004–2012 period, we determine that (1) there is slight synchronicity among different net primary production components in their response to changes in rainfall. Only litterfall showed strong correlations among the different forest groups studied, but their correlation with rainfall was poor. Moreover, mortality rates were positive correlated only with the white-sand forest (loamy sand), but there were differences between the terra-firme and flooded forest in terms of mortality rates for the 2005 and 2011 droughts. Our results suggest that differences in soils and forest structure play an important role in determining their response to changes in climate. (2) Above and belowground forest components showed different temporal trends among forests. Under drought events, the forests responded asynchronously allocating carbon to a specific forest component (e.g., fine-root production in sandy forest or litterfall or wood growth in clay forests). Specific soil characteristics such as their propensity to waterlogging were important factors in determining the degree of belowground NPP. (3) Leaf area index, despite showing some correlation among forests, did not reflect the observed variations in aboveground NPP components. This suggests high uncertainty of LAI as a measure of changes in the aboveground NPP components related to rainfall fluctuations.

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Literature Cited

Adeney, J. M., N. L. Christensen, A. Vicentini, and M. Cohn-Haft. 2016. White-sand ecosystems in Amazonia. Biotropica 48:7–23.

Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:art129.

Brando, P. M., S. J. Goetz, A. Baccini, D. C. Nepstad, P. S. Beck, and M. C. Christman. 2010. Seasonal and interannual variability of climate and vegetation indices across the Amazon. Proceedings of the National Academy of Sciences USA 107:14685–14690.

Brando, P. M., D. C. Nepstad, E. A. Davidson, S. E. Trumbore, D. Ray, and P. Camargo. 2008. Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. Philosophical Transactions of the Royal Society B: Biological Sciences 363:1839–1848.

Brienen, R. J. W., et al. 2015. Long-term decline of the Amazon carbon sink. Nature 519:344–348.

Chave, J., et al. 2010. Regional and seasonal patterns of litterfall in tropical South America. Biogeosciences 7:43–55.

Chave, J., et al. 2019. Ground data are essential for biomass remote sensing missions. Surveys in Geophysics 40:863–880.

Chave, J., R. Condit, S. Aguilar, A. Hernandez, S. Lao, and R. Perez. 2004. Error propagation and scaling for tropical forest biomass estimates. Philosophical Transactions of the Royal Society B: Biological Sciences 359:409–420.

Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Thomlinson, and J. Ni. 2001. Measuring net primary production in forests: concepts and field methods. Ecological Applications 11:356–370.

Corlett, R. T. 2011. Impacts of warming on tropical lowland rainforests. Trends in Ecology and Evolution 26:606–613.

da Costa, A. C. L., et al. 2010. Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. New Phytologist 187:579–591.

Davidson, E. A., et al. 2012. The Amazon basin in transition. Nature 481:321–328.

Dickey, D. A., and W. A. Fuller. 1979. Distribution of the estimators for autoregressive time series with a unit root. Journal of the American Statistical Association 74:427–431.

Engelbrecht, B. M. J., L. S. Comita, R. Condit, T. A. Kursar, M. T. Tyree, B. L. Turner, and S. P. Hubbell. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447:80–83.

Fine, P. V. A., R. García-Villacorta, N. C. A. Pitman, I. Mesones, and S. W. Kembel. 2010. A floristic study of the white sand forests of Peru. Annals of the Missouri Botanical Garden 97:283–305.

Gale, N., and A. S. Barfod. 1999. Canopy tree mode of death in a western Ecuadorian rain forest. Journal of Tropical Ecology 15:415–436.

Girardin, C. A. J., et al. 2014. Seasonality of net primary productivity along an Andean altitudinal transect in Peru. Journal of Tropical Ecology 30:503–519.

Guisande, C., A. Barreiro, I. Maneiro, I. Riveiro, A. R. Vergara, and A. Vaamonde. 2006. Tratamiento de datos. Ediciones Díaz de Santos, Madrid, Spain.

Guisande, C., J. Heine, J. González-DaCosta, and E. García-Roselló. 2014. RWizard software. University of Vigo, Vigo, Spain.

Guisande, C., and A. Vaamonde. 2012. Gráficos estadísticos y mapas con R. Ediciones Díaz de Santos, Madrid, Spain.

Guisande, C., A. Vaamonde, and A. Barreiro. 2011. Tratamiento de datos con R, SPSS y STATISTICA, Ediciones Díaz de Santos, Madrid, Spain.

Hofhansl, F., J. Kobler, J. Ofner, S. Drage, E. M. Pölz, and W. Wanek. 2014. Sensitivity of tropical forest aboveground productivity to climate anomalies. Global Biogeochemical Cycles 28:1437–1454.

Hyndman, R. J., G. Athanasopoulos, S. Razbash, D. Schmidt, Z. Zhou, Y. Khan, C. Bergmeir, and E. Wang. 2019. Forecasting functions for time series and linear models. R package version 8.9. https://CRAN.R-project.org/package=forecast

Hyndman, R. J., and Y. Khandakar. 2008. Automatic time series forecasting: the forecast package for R. Journal of Statistical Software 27:1–22.

Jiménez, E. M., et al. 2014. Edaphic controls on ecosystem-level carbon allocation in two contrasting Amazon forests. Journal of Geophysical Research: Biogeosciences 119:1820–1830.

Jimenez, E. M., F. H. Moreno, M. C. Peñuela, S. Patino Gallego, and J. Lloyd. 2009. Fine root dynamics for forests on contrasting soils in the Colombian Amazon. Biogeosciences 6:2809–2827.

Lewis, S. L., P. M. Brando, O. L. Phillips, G. F. M. van der Heijden, and D. Nepstad. 2011. The 2010 Amazon drought. Science 331:554.

Malhi, Y., et al. 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. Global Change Biology 10:563–591.

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

Malhi, Y., C. Doughty, and D. Galbraith. 2011. The allocation of ecosystem net primary productivity in tropical forests. Philosophical Transactions of the Royal Society B 366:3225–3245.

McDowell, N., et al. 2018. Drivers and mechanisms of tree mortality in moist tropical forests. New Phytologist 219:851–869.

Medlyn, B. E. 2011. Comment on "Drought-induced reduction in global terrestrial net primary production from 2000 through 2009". Science 333:1093.

Meir, P., et al. 2009. The effects of drought on Amazonian rain forests. Pages 429–449 *in* M. Keller, M. Bustamante, J. Gash, and P. Silva-Dias, editors. Amazonia and global change. Geophysical Monograph Series. American Geophysical Union, Washington, D.C., USA.

Meir, P., and F. I. Woodward. 2010. Amazonian rain forests and drought: response and vulnerability. New Phytologist 187:553–557.

Nemani, R. R., C. D. Keeling, H. Hashimoto, W. M. Jolly, S. C. Piper, C. J. Tucker, R. B. Myneni, and S. W. Running. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300:1560–1563.

Nepstad, D. C., et al. 2002. The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. Journal of Geophysical Research: Atmospheres 107:LBA 53-1–LBA 53-18.

Nepstad, D. C., I. M. Tohver, R. David, M. Paulo, and G. Cardinot. 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. Ecology 88:2259–2269.

Parolin, P., J. Adis, W. A. Rodrigues, I. Amaral, and M. T. F. Piedade. 2004. Floristic study of an igapó floodplain forest in Central Amazonia, Brazil (Tarumã-Mirim, Rio Negro). Amazoniana 18: 29–47.

Phillips, O. L., et al. 2009. Drought sensitivity of the Amazon rainforest. Science 323:1344–1347.

Phillips, O. L., et al. 2010. Drought-mortality relationships for tropical forests. New Phytologist 187:631–646.

Potter, C., S. Klooster, C. Hiatt, V. Genovese, and J. C. Castilla-Rubio. 2011. Changes in the carbon cycle of Amazon ecosystems during the 2010 drought. Environmental Research Letters 6:034024.

Quesada, C. A., et al. 2010. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. Biogeosciences 7:1515–1541.

Quesada, C. A., et al. 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences 9:2203–2246.

Quesada, C. A., and J. Lloyd. 2016*a*. Interactions between biosphere, atmosphere, and human land use in the Amazon Basin: an introduction. Pages 267–300 *in* L. Nagy, P. Artaxo, and B. R. Forsberg, editors. Interactions between biosphere, atmosphere, and human land use in the Amazon Basin. Ecological Studies 227. Springer, Berlin, Germany.

Quesada, C. A., and J. Lloyd. 2016*b*. Soil-vegetation interactions in Amazonia. *In* L. Nagy, B. R. Forsberg, and P. Artaxo, editors. Interactions between biosphere, atmosphere and human land use in the Amazon Basin. Springer Berlin Heidelberg, Berlin, Germany.

Quesada, C. A., J. Lloyd, L. O. Anderson, N. M. Fyllas, M. Schwarz, and C. I. Czimczik. 2011. Soils of Amazonia with particular reference to the RAINFOR sites. Biogeosciences 8:1415–1440.

R Development Core and Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rammig, A., T. Jupp, K. Thonicke, B. Tietjen, J. Heinke, S. Ostberg, W. Lucht, W. Cramer, and P. Cox. 2010. Estimating the risk of Amazonian forest dieback. New Phytologist 187:694–706.

Reichstein, M., et al. 2013. Climate extremes and the carbon cycle. Nature 500:287–295.

Rossetti, D. F., R. Gribel, P. M. Toledo, S. H. Tatumi, M. Yee, D. R. G. Tudela, C. S. Munita, and L. de Souza Coelho. 2018. Unfolding long-term Late Pleistocene-Holocene disturbances of forest communities in the southwestern Amazonian lowlands. Ecosphere 9:e02457.

Rowland, L., et al. 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. Nature 528:119–122.

Saatchi, S., S. Asefi-Najafabady, Y. Malhi, L. E. O. C. Aragão, L. O. Anderson, R. B. Myneni, and R. Nemani. 2013. Persistent effects of a severe drought on Amazonian forest canopy. Proceedings of the National Academy of Sciences USA 110: 565–570.

Saleska, S. R., K. Didan, A. R. Huete, and H. R. da Rocha. 2007. Amazon forests green-up during 2005 drought. Science 318:612.

Samanta, A., M. H. Costa, E. L. Nunes, S. A. Vieira, L. Xu, and R. B. Myneni. 2011. Comment on "Drought-induced reduction in global terrestrial net primary production from 2000 through 2009". Science 333:1093.

Samanta, A., S. Ganguly, H. Hashimoto, S. Devadiga, E. Vermote, Y. Knyazikhin, R. R. Nemani, and R. B. Myneni. 2010. Amazon forests did not green-up during the 2005 drought. Geophysical Research Letters 37:L05401.

Samanta, A., S. Ganguly, E. Vermote, R. R. Nemani, and R. B. Myneni. 2012. Interpretation of variations in MODIS-measured greenness levels of Amazon forests during 2000 to 2009. Environmental Research Letters 7:24018.

Sierra, C. A., E. M. Jiménez, B. Reu, M. C. Peñuela, A. Thuille, and C. A. Quesada. 2013. Low vertical transfer rates of carbon inferred from radiocarbon analysis in an Amazon Podzol. Biogeosciences 10:3455–3464.

Thien, S. J. 1979. A flow diagram for teaching texture by feel analysis. Journal of Agronomic Education 8:54–55.

Trapletti, A., and K. Hornik. 2019. tseries: time series analysis and computational finance. R package version 0.10-47. https://CRAN.R-project.org/package=tseries

Vogt, K. A., D. J. Vogt, and J. Bloomfield. 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forest at an ecosystem level. Plant and Soil 200:71–89.

Williamson, G. B., W. F. Laurance, A. A. Oliveira, P. Delamônica, C. Gascon, T. E. Lovejoy, and L. Pohl. 2001. Amazonian tree mortality during the 1997 El Niño drought. Conservation Biology 14:1538–1542.

Zeng, N., J.-H. Yoon, J. A. Marengo, A. Subramaniam, C. A. Nobre, A. Mariotti, and J. D. Neelin. 2008. Causes and impacts of the 2005 Amazon drought. Environmental Research Letters 3:14002.

Zhao, M., and S. W. Running. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science 329:940–943.

Zhou, X., Y. Fu, L. Zhou, B. Li, and Y. Luo. 2013. An imperative need for global change research in tropical forests. Tree Physiology 33:903–912.