RESEARCH ARTICLE

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Shock and stabilisation following long-term drought in tropical forest from 15 years of litterfall dynamics

Lucy Rowland[1] iD | Antonio C. L. da Costa[2] | Alex A. R. Oliveira[3] | Samuel S. Almeida[3†] | Leandro V. Ferreira[3] | Yadvinder Malhi[4] | Dan B. Metcalfe[5] | Maurizio Mencuccini[6,7] | John Grace[8] | Patrick Meir[8,9]

[1]Department of Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK; [2]Instituto de Geociências, Universidade Federal do Pará, Belém, Brazil; [3]Museu Paraense Emílio Goeldi, Belém, Brazil; [4]Environmental change Institute, University of Oxford, Oxford, UK; [5]Physical Geography and Ecosystem Science, Lund University, Lund, Sweden; [6]CREAF, Cerdanyola del Vallés, Spain; [7]ICREA, Barcelona, Spain; [8]School of GeoSciences, University of Edinburgh, Edinburgh, UK and [9]Research School of Biology, Australian National University, Canberra, Australia

Correspondence
Lucy Rowland
Email: l.rowland@exeter.ac.uk

Abstract

1. Litterfall dynamics in tropical forests are a good indicator of overall tropical forest function, indicative of carbon invested in both photosynthesising tissues and reproductive organs such as flowers and fruits. These dynamics are sensitive to changes in climate, such as drought, but little is known about the long-term responses of tropical forest litterfall dynamics to extended drought stress.

2. We present a 15-year dataset of litterfall (leaf, flower and fruit, and twigs) from the world's only long-running drought experiment in tropical forest. This dataset comprises one of the longest published litterfall time series in natural forest, which allows the long-term effects of drought on forest reproduction and canopy investment to be explored.

3. Over the first 4 years of the experiment, the experimental soil moisture deficit created only a small decline in total litterfall and leaf fall (12% and 13%, respectively), but a very strong initial decline in reproductive litterfall (flowers and fruits) of 54%. This loss of flowering and fruiting was accompanied by a de-coupling of all litterfall patterns from seasonal climate variables. However, following >10 years of the experimental drought, flower and fruiting re-stabilised at levels greater than in the control plot, despite high tree mortality in the drought plot. Litterfall relationships with atmospheric drivers were re-established alongside a strong new apparent trade-off between litterfall and tree growth.

4. *Synthesis*. We demonstrate that this tropical forest went through an initial shock response during the first 4 years of intense drought, where reproductive effort was arrested and seasonal litterfall patterns were lost. However, following >10 years of experimental drought, this system appears to be re-stabilising at a new functional state where reproduction is substantially elevated on a *per* tree basis; and there is

a new strong trade-off between investment in canopy production and wood production.

1 | INTRODUCTION

Tropical rainforests are responsible for over 40% of global terrestrial photosynthesis (Beer, Reichstein, Tomelleri, & Ciais, 2010) and a large fraction (20%–50%) of this productivity is invested in production and maintenance of the forest canopy (Malhi, Doughty, Goldsmith, & Metcalfe, 2015). Canopy biomass production (of leaves, flowers and fruit) is typically the largest component of net primary production (NPP) in tropical forests, and as a result, litterfall has been shown to be a good proxy for estimates of NPP on annual or multiannual scales (Malhi, Doughty, & Galbraith, 2011). Moreover, the seasonal dynamics of the canopy carbon pool play a central role in controlling forest function; leaf turnover directly influences photosynthetic production (Myneni, Yang, Nemani, & Huete, 2007; Wu, Albert, Lopes, & Restrepo-Coupe, 2016), and flower and fruit production strongly influence reproduction and forest succession. Given that the turnover rates of leaves and reproductive organs are also sensitive to exogenous changes in climate (Aragão, Malhi, Metcalfe, & Silva-Espejo, 2009; Chave, Navarrete, Almeida, & Alvarez, 2010; Wagner, Herault, Bonal, & Stahl, 2016), they may also be good indicators of how the whole forest ecosystem responds to climate shifts. However, how canopy production responds to long-term changes or inter-annual variability in climate remains poorly explored, despite predictions of increasing climate variability and extremes, alongside long-terms trends towards hotter and seasonally drier climates in many parts of the tropics (Cai, Borlace, Lengaigne, & van Rensch, 2014; Duffy, Brando, Asner, & Field, 2015).

Litterfall is comprised of three main components, leaves, reproductive material (flowers and fruits) and fine woody material (twigs, generally <2 cm diameter). Investment into photosynthetic production (leaves) is the largest of these three, with leaf fall typically comprising around 71% of total litterfall across South American tropical forests (Chave et al., 2010). Investment into reproductive material is estimated to be typically only 9% of total litterfall in South American forests; however, there is much variance in this value among forests, with greater resource availability often leading to a larger allocation to the production of flowers and fruits (Chave et al., 2010). Leaf and reproductive litterfall are highly seasonal within tropical humid forests and likely to be strongly influenced by intra- and inter-annual variability in climate, potentially leading to high variance over the short term (Chave et al., 2010; Girardin, Malhi, Doughty, & Metcalfe, 2016; Wagner et al., 2016). However, determining if total litterfall and its components are controlled by particular exogenous climate drivers, or endogenous biotic controls, is complex as these variables are often cross-correlated

(e.g. Wagner et al., 2016). For example, the production of new leaves generally occurs at the transition from wet to dry season, as the forest creates new leaves with greater water-use efficiency and photosynthetic capacity to maximise dry season photosynthetic production or minimise pathogen and herbivory pressure (Carswell et al., 2002; Girardin et al., 2016; Wu et al., 2016). However, the production of new leaves is also positively related to the abscission of old leaves, which can be triggered by low water availability and high evaporative demand in tropical forests (Bi, Knyazikhin, Choi, & Park, 2015; Borchert, Calle, Strahler, & Baertschi, 2015; Wright & Cornejo, 1990), and negatively correlated with carbon investment in woody growth (Aragão et al., 2009; Doughty, Metcalfe, Girardin, & Amezquita, 2015; Wagner et al., 2016).

The investments of carbon into canopy and woody growth components comprise the largest allocation of fluxes in tropical forest trees (Aragão et al., 2009; Malhi, Aragao, Metcalfe, & Paiva, 2009), and their timing and magnitude are intrinsically linked. Woody growth is also strongly linked to water availability, with cell expansion being more sensitive to water restriction than photosynthesis (Körner, 2013), and sometimes becoming dormant in periods of restricted water availability (Krepkowski, Brauning, Gebrekirstos, & Strobl, 2011; Makinen, Seo, Nojd, & Schmitt, 2008). Seasonal growth restrictions may necessitate heavy carbon investment in woody tissue growth during wet periods, restricting investment into foliar production. As a consequence, in addition to its influence on overall productivity (Meir & Woodward, 2010) and its seasonal dynamics (Wagner et al., 2016), water availability likely acts as a key control on the differential allocation of photosynthate to different tissues in tropical trees.

Restrictions in water availability are thought to act as a direct constraint on leaf turnover in tropical forests receiving <2,000 mm rainfall (Wagner et al., 2016), although many studies contradict this, suggesting radiation rather than water is the key driver of litterfall patterns, even in drier tropical forests (Borchert et al., 2015; Girardin et al., 2016; Myneni et al., 2007). Water limitation may also have a positive effect on reproductive output, potentially increasing production in dry tropical forests (Lohbeck et al., 2015) and driving mass flowering (masting) events in the ever-wet forests of SE Asia (Sakai, Harrison, Momose, & Kuraji, 2006). Given the control of flowering and leaf turnover on long-term forest succession, productivity and seasonal dynamics, the response of litterfall to drought may act as a good indicator, or early warning signal, of the likely response of the whole system, from resistance, through resilience, to potential long-term shifts in behaviour (Hirota, Holmgren, Van Nes, & Scheffer, 2011; Scheffer, Bascompte, Brock, & Brovkin, 2009). For

example, a long-term decline of flowering would suggest that the current species composition is not viable under long-term drought, and the system must shift to a new species composition. To determine such changes, long-term datasets are essential so that short-term responses to a climatological disturbance can be disentangled from long-term effects which may permanently shift characteristic ecosystem functioning (Hirota et al., 2011; Lenton, 2011). Short-term natural drought events, such as those which occurred across Amazonia in 2005, 2010 and 2015 (Feldpausch, Phillips, Brienen, & Gloor, 2016; Marengo, Tomasella, Alves, Soares, & Rodriguez, 2011; Phillips, van der Heijden, Lewis, & Lopez-Gonzalez, 2010), may therefore be insufficient to assess the prolonged ecosystem response to climatic change. Long-term climate predictions favour some form of extended drought stress in Amazonia, through secular change and/or punctuated extremes (Boisier, Ciais, Ducharne, & Guimberteau, 2015; Duffy et al., 2015; Fu, Yin, Li, & Arias, 2013), and so to understand their impact on carbon allocation to the forest canopy it is necessary to also explore the response to long-term reductions in water availability.

In this study, we present the one of the longest published time series of litterfall from a tropical forest (2001–2016). We separate the litterfall into leaves, reproductive parts and twigs, and use a long-running (14 years) large-scale (1 ha) soil moisture reduction experiment to contrast unmodified natural forest with long-term drought-stressed forest. Using these data, we examine: (1) the response to the initial (i.e. short-term) effect of a 50% reduction in canopy throughfall; (2) how the imposed soil moisture deficit alters long-term relationships among canopy production and seasonal and inter-annual growth and climate variables; and (3) whether current evidence indicates a long-term shift characterised by the forest re-stabilising a new functional state or whether there is a continuous change in litterfall following 15 years of soil drought stress.

2 | MATERIALS AND METHODS

2.1 | Site

The study plots are located within the Caxiuanã National Forest Reserve in the eastern Amazon (1°43′S. 51°27W). The site has a mean rainfall of 2,000–2,500 mm/year, a pronounced dry season between June and November, where rainfall is below 100 mm/month. The two plots are part of a long-term throughfall exclusion experiment (TFE). The experiment consists of two 1 ha plots located on old growth *terra firme* evergreen forest on yellow oxisol soils (Ruivo & Cunha, 2003). The TFE plot has been covered with plastic panels supported at 1–2 m height which have excluded 50% of the incoming canopy throughfall from 2002 to present day (da Costa, Galbraith, Almeida, & Portela, 2010; Meir, Wood, Galbraith, & Brando, 2015; Rowland, da Costa, et al., 2015; Rowland, Lobo-do-Vale, et al., 2015). To prevent lateral through-flow of water from the surrounding soil, the TFE plot was trenched to 1–2 m depth (see da Costa et al., 2010; Rowland, Lobo-do-Vale, et al., 2015 for further details). Less than 50 m from the TFE plot a corresponding 1 ha control plot, also trenched in 2001, was set

up, experiencing normal rainfall and no experimental throughfall exclusion. Litterfall has been monitored on these plots since 2001.

2.2 | Meteorological data

Precipitation, relative humidity, global solar radiation and air temperature were measured at the top of a 40-m tower located in the control plot. Air temperature, relative humidity, solar radiation and rainfall were monitored half hourly using HC2S3 and CM3 sensors, and a tipping bucket rain gauge (Campbell Scientific, Logan, USA), respectively. These data were available on an hourly time-scale from 2001 to 2016, gaps in the data <12 hr were filled using linear interpolation, gaps >12 hr were filled using the average value from the same time period in the three preceding and subsequent years. The percentage of gap-filled data per variable did not exceed 12.8%. Following this, data were averaged into monthly means, or monthly totals in the case of precipitation.

Soil moisture content was monitored on both the TFE and control plots. On each plot, a soil access pit was instrumented with volumetric soil water content sensors (CS616, Campbell Scientific, Logan, USA), placed at depths of 0, 0.5, 1, 2.5 and 4 m, and soil moisture was monitored every hour (*cf*. Fisher, Williams, Ruivo, & Da Costa, 2008; for full methodology). Values of volumetric soil water content values were converted into estimates of relative extractable water (REW) following the methodology of Meir et al. (2015), using the lowest value from the TFE and the highest point from the control plot as the minimum and maximum reference points, respectively. REW was aggregated across the first 2 m of soil depth, and averaged into monthly values to correspond to the litterfall time series.

2.3 | Litterfall data

Litter was collected in litter traps arranged in a grid across the two plots. From 2001 to 2009, litterfall was collected on a monthly basis from 20 litter traps spaced evenly across the plots, and from 2009 onwards, it was collected on a two-weekly basis from 25 evenly spaced litter traps. Across this time period, litter-trap size varied from 0.25 to 1 m^{-2}. However, all data are standardised to 1 m^{-2} and presented on a monthly average basis, to remove effects of litter-trap size and collection frequency changes from our data. Litter was collected from all traps and sorted into leaf material, reproductive material (flowers and fruits), woody material <2 cm in diameter (twigs) and non-identifiable plant material, which comprised only a small fraction of annual litterfall, on average (3.7%). Following separation, the material was then dried to a constant mass in an oven and weighed to calculate biomass.

The availability of monthly litterfall data on each plot is shown in Figure 1c. To create annual litter totals for missing months, data series were gap-filled by linear interpolation using three consecutive months on the each of the control and TFE plots. However, from October 2006 to May 2007, data collection was stopped across all plots and so annual totals were not calculated for 2006 and 2007. From 2007 to the end of 2009, litterfall values across all plots were incorrectly recorded and therefore data from June 2007 to December 2009 were
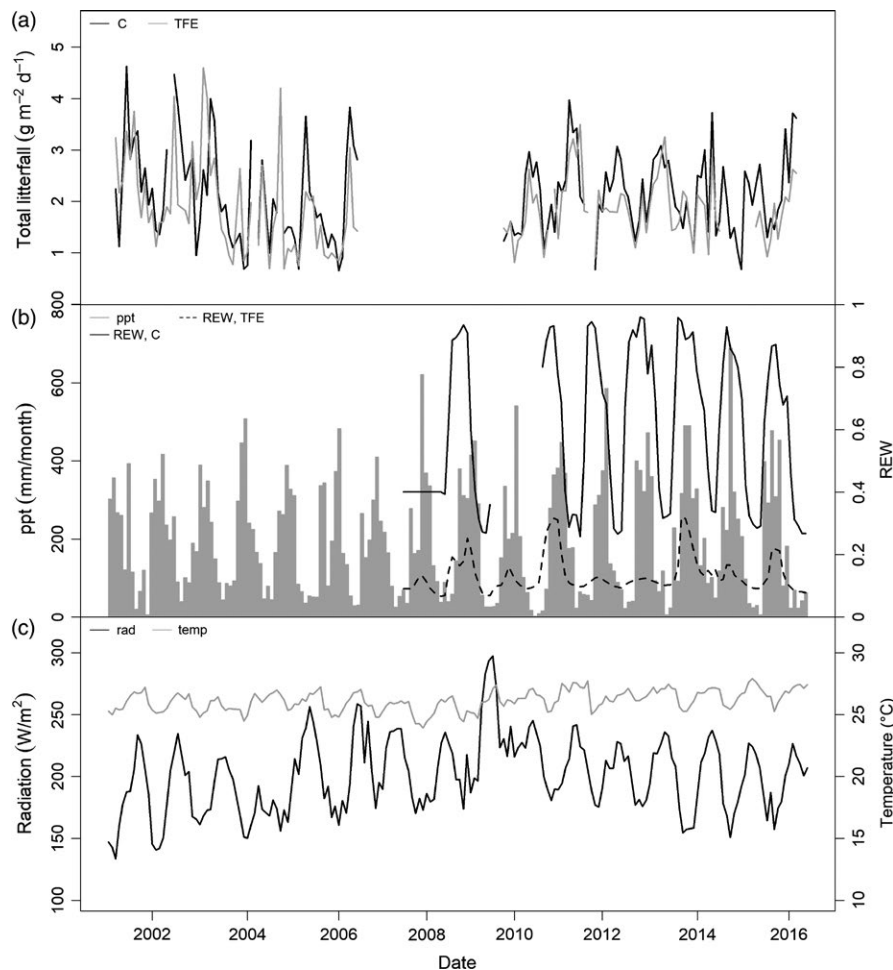
FIGURE 1 Changes in total litterfall (g m^{-2} day^{-1}) on the control (C, black) and TFE (grey, panel a), mean monthly precipitation (mm/month grey bars) and mean monthly relative extractable water (REW, unitless) on the control (solid line) and TFE (dashed line; panel b), and finally, mean monthly radiation (W/m^2) and mean monthly temperature (°C), during the 2001–2016 study period (panel c)

excluded from this analysis. Finally, data are missing on the TFE plot from January to September 2015 and annual totals could not be calculated. Despite these gaps, this dataset still comprises one of the longest running published litterfall datasets for any tropical forest.

2.4 | Growth rate data

Mean plot-level stem diameter increment every 3 months from 2005 onwards was taken from (Rowland, da Costa, et al. 2015; Rowland, Lobo-do-Vale, et al. 2015) and converted to units of cm/day. To match these data, monthly litterfall was also converted to three-monthly averages. Accounting for the data gap in the litterfall time series (Figure 1a, Table S1), correlations between growth and litterfall were performed for 2010–2016. Litterfall and growth data between 2010 and 2016 were also converted to annual mean values to explore inter-annual trade-offs between investment in canopy and stem growth.

2.5 | Statistical analysis

All statistical analyses were performed within the statistical package R (R Core Team, 2014). Linear correlations were performed between log-transformed values of leaf and reproductive litterfall values from

the Control and TFE, and the meteorological and soil REW data. To remove autocorrelation from these seasonal relationships, the log-transformed values of leaf and reproductive litterfall lagged by 1 month were also included as independent variables. ACF plots were used to ensure that a lag of 1 month removed all autocorrelation in the dependent variables. To estimate if there were lagged correlations between litterfall and environmental variables, a cross-correlation analysis was used (ccf function in R, following Brockwell & Davis, 1991) to pick the optimum lag of between zero to 6 months of each environmental variable. For correlations with climate variables, the full time series of available litterfall data were used; however, for correlations with REW, there was only overlap between the datasets from January 2010 to December 2016. Autocorrelation analysis also was performed on the residuals of each single linear model to ensure no autocorrelation existed in any of the models. Using the lags from the cross-correlation analysis, multivariate linear models of leaf and reproductive litterfall were created using precipitation, radiation, REW, relative humidity or temperature, as independent variables, alongside the litterfall variable lagged by 1 month to remove autocorrelation. Backward and forward stepwise regressions were used, comparing models using the Akaike Information Criterion (AIC), to identify the model with the highest likelihood using the least number of variables. To explore inter-annual controls of climate and soil moisture
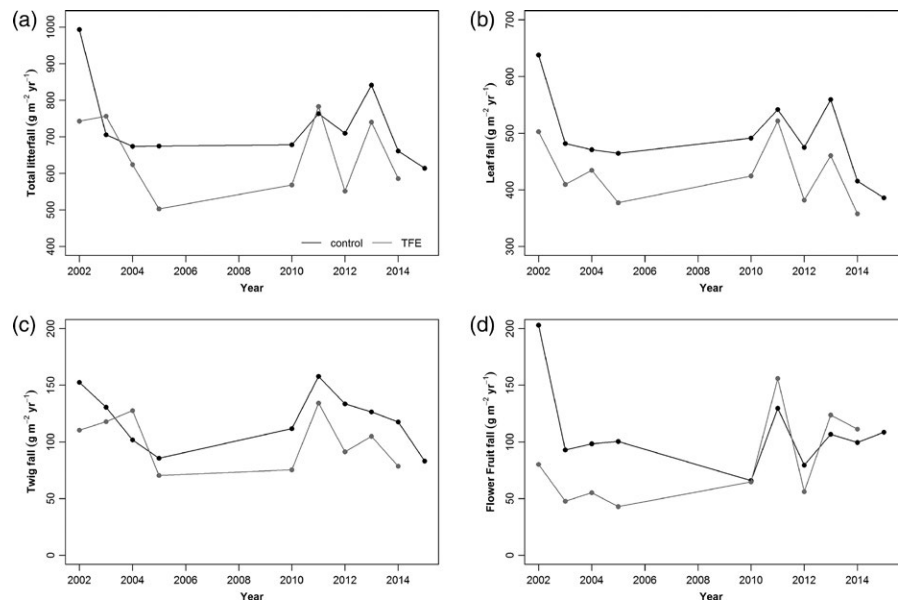
FIGURE 2 Annual totals of total litterfall (g m^{-2} year^{-1}) (a) leaf fall (g m^{-2} year^{-1}) (b) twig fall (g m^{-2} year^{-1}) (c) and flower and fruitfall (reproductive litterfall, g m^{-2} year^{-1}) (d) on the control (black bars) and TFE (grey bars) for the years with full data (see Section 2)

on litterfall, correlations between meteorological, REW and litterfall variables were also performed on an annual time-scale by taking mean annual values.

3 | RESULTS

The study area experiences a strong seasonality in moisture availability with rainfall, relative humidity and REW (control plot) increasing substantially during the 6-month wet season, which generally starts between December and January, and ends between June and July (Figure 1b,c). Seasonality in global solar radiation (W/m^2) showed the opposite trend to precipitation, increasing in the dry season and declining in the wet (Figure 1b). The artificially imposed drought on the TFE severely restricted REW (Figure 1a); wet season REW values on the TFE were below the dry season values on the control and the seasonal amplitude on the TFE was substantially smaller, although with greater proportional inter-annual variation.

The control plot had a total litterfall of 731 ± 35 g m^{-1} year^{-1} (Figure 2a), 67% of which was leaf fall. During the first 4 years of the TFE experiment, total litterfall and leaf fall on the TFE were 650 ± 35 g m^{-2} year^{-1} and 430 ± 19 g m^{-2} year^{-1}, respectively, and this represented an overall reduction with respect to the control forest of 12% and 13%, respectively. In contrast, during the same period, reproductive litterfall was 54% lower on the TFE than on the control plot (56 ± 8 g m^{-2} year^{-1}, compared to 123±26 g m^{-2} year^{-1}). From 2010 onwards, however, the reproductive litterfall on the TFE was on average greater than on the control (Figure 2d). This resulted in reproductive litterfall changing from 9 ± 1% of total litterfall on the TFE during the first 3 years of the experiment to 15 ± 2% during the last 3 years of the experiment for which data are available all year (2012–2014, Figure 3). Intra-annual variability was also greatest in reproductive litterfall, which varied by c. 300% on the control and the TFE. Inter-annual variability in total litterfall on both plots remained

low; however, reflecting low inter-annual variability in leaf and twig fall (Figure 2a,c).

The high inter-annual variability in reproductive litterfall on the TFE was caused by a complete loss of the dry season peak in flowering and fruiting from August to October for the first 3 years of the experiment (2002–2005, Table 1). However, following 10 years of drought, reproductive litterfall on the TFE recovered, with a much stronger seasonal peak in September compared to the control forest (Figure 3b). Leaf fall peaked before reproductive litterfall from June to July (Figure 3a,b). On the TFE, peak leaf fall declined to substantially below that of the control plot following long-term drought (1.8 ± 0.2 g m^{-2} day^{-1} and 2.3 ± 0.2 g m^{-2} day^{-1}, respectively, Figure 3a). In the first 4 years of the experiment, however, peak leaf fall remained similar on both plots, but on the TFE it was more tightly restricted to July, declining sharply in October to create significantly lower leaf fall on the TFE during September to November relative to the control plot, and relative to the recent average leaf fall rate on the TFE (Figure 3a). In contrast to the leaf and reproductive litterfall, there was little consistent or significant change in twig fall between the plots in terms of timing or mass (Figure 3).

Strong shifts in seasonality of leaf and reproductive litterfall on the TFE resulted in seasonal correlations with meteorological drivers (air temperature, radiation, air humidity and precipitation) being absent during the early stage of the experiment (2002–2005) compared to the control forest (Table 1). These seasonal relationships returned, however, in the latter years of the experiment (2012:2016) and were similar to those which exist on the control (Table 1). However, the seasonal changes observed in the later stages of the TFE experiment for leaf and reproductive litterfall (Table 1) resulted in a stronger correlation of leaf fall with radiation on the TFE (r^2 = .27, Table 1) than on the control (r^2 = .19, 4c), and a stronger correlation of reproductive litterfall with air temperature (r^2 = .27 TFE, r^2 = .12 Control). Correlations performed between litterfall and REW from 2010 onwards (when REW data became
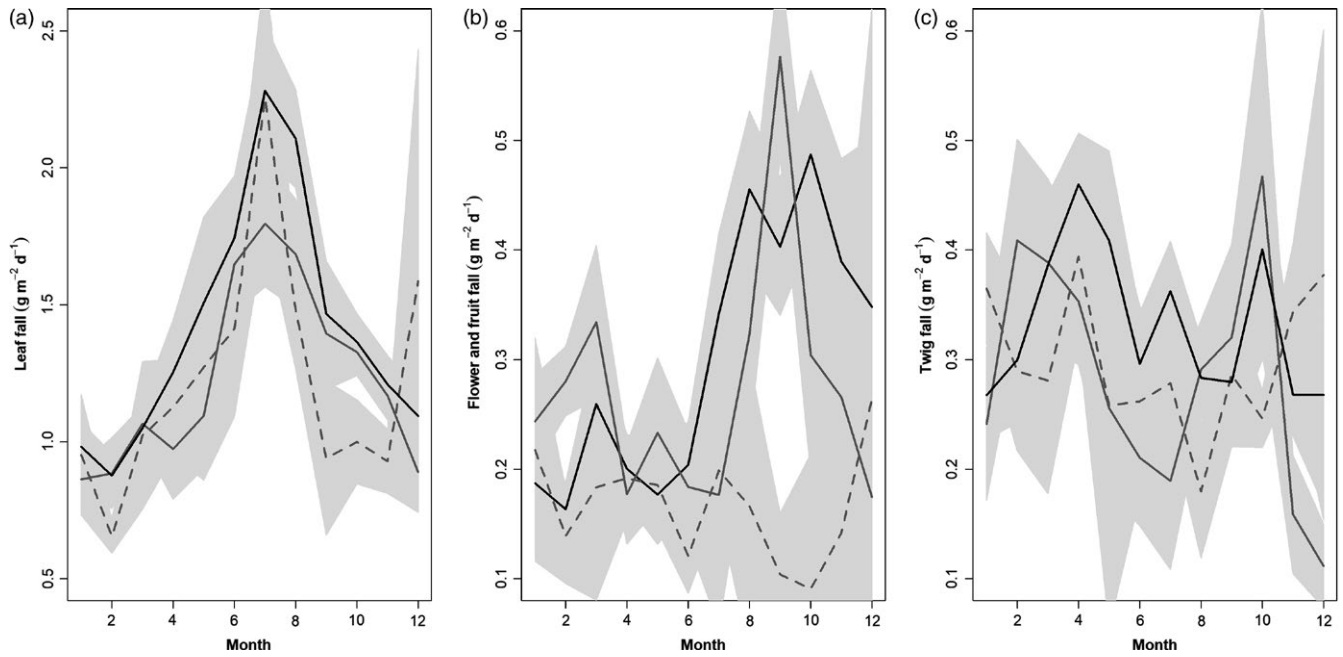
FIGURE 3 Mean daily leaf fall (g m^{-2} day^{-1}) (a) flower and fruit fall (g m^{-2} day^{-1}) (b) and twig fall (g m^{-2} day^{-1}) (c) for the control plot (2001–2016, black lines), the first 4 years of the TFE (2002–2005, grey dashed lines) and the final 5½ years of the TFE (2012–2016, grey solid lines). Grey-shaded areas indicate the standard error around the lines

TABLE 1 Linear relationships of logged monthly environmental variables (temperature (temp, °C), relative humidity (RH, %), radiation (Rad, W/m^2), precipitation (PPT, mm/month) and relative extractable water (REW) against logged monthly mean leaf fall and flower and fruit fall on the control, the early period on the TFE (2002:2005) and the later period on the TFE (2012:2016). Numbers in bold show the R^2 values of relationships significant at p-values of .01–.05 (*) and <.01 (**). Non-bold numbers show the number of lags used in the environmental variable which were determined by the ccf function in R (see Section 2). To remove autocorrelation, all logged litterfall quantities were regressed against their own values at a lag of 1 month, alongside environmental variables (see Section 2)

Variables	Temp	RH	Rad	PPT	REW
Control leaf	0.32**, 0	0.30**, 0	0.30**, 0	0.28**, 0	0.45**, 4
Control F + F	0.25**, 2	0.24**, 0	0.23**, 0	0.55**, 0	0.21**, 0
TFE early Leaf	0.20*, 0	NA	NA	NA	
TFE early F + F	NA	NA	NA	NA	
TFE late leaf	0.22**, 0	0.27**, 0	0.29**, 0	0.23**, 0	0.26**, 4
TFE late F + F	0.28**, 3	0.26**, 0	0.26**, 0	0.27**, 0	0.28**, 0

available), demonstrated REW was the strongest environmental predictor of leaf fall on both plots, and of reproductive litterfall on the Control but not on the TFE (Table 1). A very weak positive correlation between REW and reproductive litterfall existed on the TFE (r^2 = .07) contrasting a stronger negative correlation between REW and reproductive litterfall on the control (r^2 = .22). When stepwise multivariate linear model analysis was performed using the environmental data and lags from Table 1, and the litterfall variable lagged by 1 month to remove autocorrelation (see Section 2), REW came out as the single best predictor of reproductive litterfall on both plots (model R^2 = .29 Control, and 0.17 TFE, p < .01). Leaf litterfall on both plots was, however, more strongly predicted with precipitation, relative humidity and REW (model R^2 = .47 control, and 0.51 TFE, p < .01). However, on the control, REW only explained 10% of

the variance in leaf fall, but this increased to 22% on the TFE, with precipitation being the other major contributor, explaining 29% and 20%, respectively, on the control and TFE.

Data for plot level growth rate were available on a three-monthly basis (see Rowland, da Costa, et al., 2015) and correlations were performed between these values and three-monthly average litterfall data. On the TFE, mean plot-level growth rate came out as the strongest correlate of leaf fall (r^2 = .47, p < −.001, Figure 4a), stronger than any other meteorological variable. In contrast, on the control plot, the strength of the correlations between leaf fall and growth rate remained low and less significant (r^2 = .17, p = .03, Figure 4a).

Despite strong seasonal effects of meteorological drivers on litterfall, no significant correlations were found between mean annual meteorological drivers or REW and annual litterfall on either plot. However,
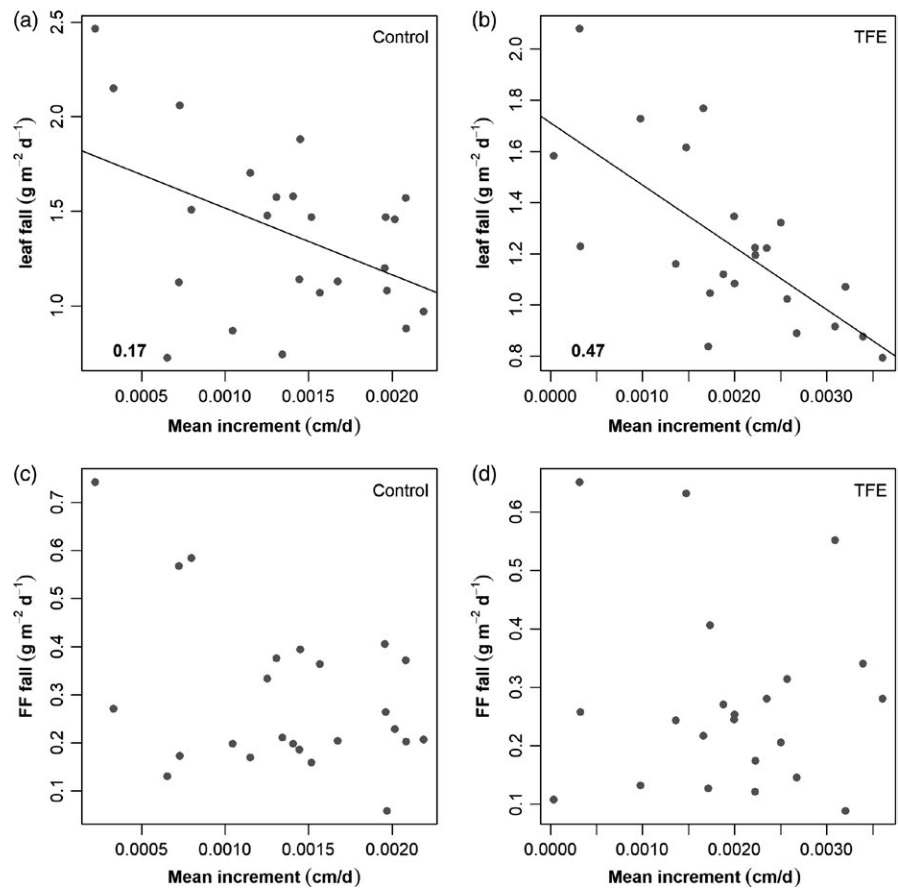
FIGURE 4 Linear correlations of mean woody growth increment every 3 months from 2010 to 2016 (cm day^{-1}) with log leaf fall on the control (g m^{-2} day^{-1}) (a) on the TFE (g m^{-2} day^{-1}) (b) and flower and log fruit fall (FF) on the control (g m^{-2} day^{-1}) (c) and TFE (g m^{-2} day^{-1}) (d) A linear line is shown if a correlation is significant at the $p < .05$ level, and the correlation coefficients for these linear lines are printed in bottom left hand side of the panel

on the TFE plot, there was a very strong annual trade-off between mean annual growth increment from 2010 to 2016 and mean annual leaf fall ($r^2 = .91$, $p < .01$), which was absent on the control plot (Figure 5).

4 | DISCUSSION

Using one of the longest published time series of litterfall data collected in a tropical forest, we demonstrate that a decadal-scale re-adjustment of reproductive capacity took place following long-term drought stress between 2001 and 2016. Our data show an initial shock response following the imposition of the TFE treatment in 2002, when the production of reproductive organs dropped dramatically and there was a de-coupling between the seasonality of litterfall and climate. However, following more than a decade of drought stress, the reproductive litterfall rates recovered to be more than on the control plot and intra-annual litterfall patterns became re-coupled, and in some cases more strongly coupled, to seasonal climate variables. Following long-term drought, the TFE-treated forest developed a strong apparent trade-off between annual investment in canopy production and woody growth.

The production of flowers and fruit is hypothesised to be closely tied to resource availability, with restrictions in reproductive capability occurring on tropical forest sites with limited resources, such as soil nutrients (Chave et al., 2010). During the 2–3 initial years of the TFE experiment, there was little change in tree mortality (da Costa et al., 2010; Meir et al., 2015; Rowland, da Costa, et al., 2015), but there was

a rapid and large (54%) decline in the production of reproductive tissues following the imposition of restricted water availability (Figure 2). This suggests that carbon investment into growth and survival, rather than reproduction, was favoured during the initial phases of the TFE, when the initial resource limitation was imposed. Following 8 years of the experiment and the start of high levels of tree mortality and biomass loss on the TFE (da Costa et al., 2010; Rowland, da Costa, et al., 2015), carbon investment in reproductive litter production increased to levels slightly greater than those on the Control (Figure 2d). This suggests that on a *per* tree basis there was progressively more relative investment towards the production of reproductive organs on the TFE, given the observed rise in mortality that led to a 20% loss of biomass on the TFE by 2008 (da Costa et al., 2010), which subsequently increased sharply after 13 years to a 40% loss of biomass by 2014 (Rowland, da Costa, et al., 2015). Such a response may be important for maintaining fitness if drier soils and reduced litter decomposition, and therefore, nutrient availability in the surface soil limit seed germination and increase seedling mortality rates (Engelbrecht, Comita, Condit, & Kursar, 2007; Poorter & Hayashida-Oliver, 2000; Poorter & Markesteijn, 2008). Connections between reproduction and drought have already been made in the tropical forest literature, for example dry forests have been observed to have a greater reproductive effort than wet forests (Lohbeck et al., 2015) and short-term droughts are known to trigger mass flowering events in Asian aseasonal forests (Sakai et al., 2006). However, we additionally demonstrate here that tropical moist forest trees exposed to soil drought-stress are able to
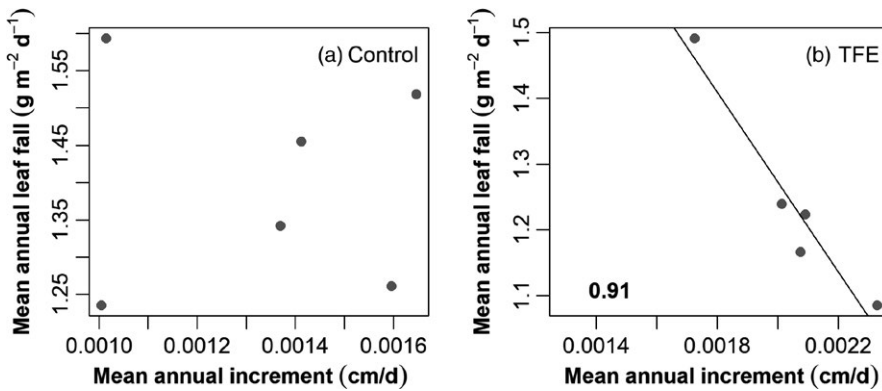
FIGURE 5 Correlations between mean daily plot-scale woody growth increment (tree circumference expansion at 1.3 m height in cm day^{-1}) and mean annual leaf fall (g m^{-2} day^{-1}) on the control (a) and the TFE (b) here a linear line is shows a significant correlation $p < .05$ level, with the correlation coefficient on left hand side of the panel

re-adjust their allocation pattern on a decadal time-scale to increase flowering and fruiting capacity, presumably maximising the reproductive success of each individual. Alongside restricted water availability, this increased reproductive output may also be related to increases in within-canopy light availability following mortality of the largest trees (da Costa et al., 2010; Rowland, da Costa, et al., 2015), and this may be driving more lower canopy trees to reproduce more abundantly.

Total annual litterfall and leaf fall (and implicitly canopy production) showed surprising little change across the lifetime of the experiment (12%–13% lower than the control in early years and later years, see Figure 3) and continued to peak in the dry season, as found across many other Amazonian sites (Chave et al., 2010; Girardin et al., 2016; Wagner et al., 2016). A previous shorter term TFE experiment in eastern Amazonia rainforest demonstrated an initial larger decline (23%) of litterfall during the third year of TFE treatment, followed by a reduced decline of 10% between the TFE and control in the fourth and final year of the experiment (Brando, Nepstad, Davidson, & Trumbore, 2008). It is notable that both experiments demonstrate only a relatively small percentage change in canopy carbon investment (as measured by total litterfall) over their lifetimes, relative to a woody biomass loss of 18%–40% (Brando et al., 2008; Rowland, da Costa, et al., 2015). This suggests that tropical forest trees prioritise the investment in canopy production during drought stress, perhaps to maximise photosynthetic gains and facilitate long-term re-adjustment to the new conditions.

Despite the relatively high rainfall on the site and the control plot not being limited by seasonal changes in water availability (Fisher, Williams, Da Costa, & Malhi, 2007), REW still comes out as the strongest single correlate of reproductive litterfall seasonality and a significant contributor to leaf fall seasonality on the control plot and particularly on the TFE plot (during the latter stages, post 2009; of Table 1). Interestingly, during the initial 4 years of the TFE, when seasonal patterns in leaf and reproductive litterfall changed substantially (Figure 3), the correlations between all meteorological variables, leaf and reproductive litterfall were lost or substantially weakened (Table 1). This indicates that the initial shock to the system may have decoupled the seasonal changes in carbon allocation on the TFE from the seasonal changes in climate, perhaps as a result of altering canopy turnover time. Following 2010, however, this coupling returned, with some seasonal correlations becoming stronger on the TFE than on the control plot (e.g. with radiation; Table 1). It seems likely therefore that

this forest is showing signs of re-stabilising its pattern of carbon allocation following an initial climate shock and a breakdown in resistance, here exemplified by a large drop in biomass (Rowland, da Costa, et al., 2015). The overall signal observed here may conceivably indicate a long-term shift towards a new ecological state characterised by alterations in the patterning of carbon allocation in response to climate.

Despite strong seasonal correlations existing between litterfall and climate (Table 1 and Chave et al., 2010; Girardin et al., 2016; Wagner et al., 2016), none of the meteorological variables analysed here at an annual time-step, or the soil moisture metric REW, were correlated strongly with inter-annual variability in leaf or reproductive litterfall. This is consistent with endogenous controls playing a larger role in determining significant changes in litterfall on annual time-scales and climate playing an indirect driving role though its influence on growth. However, in the later years of the TFE experiment (2010 onwards), there was a very strong negative correlation between mean annual growth increment on the TFE plot with leaf fall (Figure 5). This result suggests that following more than a decade of the TFE there is a very strong trade-off among years in the amount of carbon that can be invested in the canopy and in woody growth, indicating a potential decrease in overall carbon supply. On a seasonal time-scale, woody growth does correlate with leaf fall supporting the idea that there is a clear trade-off between woody growth and investment in canopy growth (Aragão et al., 2009; Doughty et al., 2015). However, the strength of this relationship is substantially higher in the TFE in the later years, compared to the control ($r^2 = .47$ and .17, respectively). Overall, these results indicate that carbon allocation trade-offs in the TFE-treated forest are stronger on a seasonal and annual time-scale, and play a far greater role than meteorology in controlling leaf carbon investment.

Using one of the longest published litterfall datasets from tropical forest, we demonstrate that following more than a decade of soil drought stress, canopy production, particularly of reproductive organs, undergoes an initial short-term rapid decline and then appears to slowly recover and re-stabilise to a position where average reproduction rates increase on the TFE, and leaf fall becomes tightly negatively correlated with tree growth on both seasonal and an inter-annual time-scales. These results are important as they show that over decadal time-scales of soil drought stress, this tropical rainforest appears to re-stabilise to a characteristic state where forest function is altered. Surviving trees improve reproductive capacity and potentially

compensate for reduced germination rates and higher seedling mortality in drier soils. Furthermore, we demonstrate that there is likely to be a direct trade-off between carbon investments in wood and leaves resulting from limitations in carbon supply. Together with the data demonstrating new correlations between inter-annual climate variability and leaf or reproductive litterfall, our overall analysis suggests that endogenous drivers may ultimately be more important than climate in controlling variation in litterfall, the allocation of NPP to leaf or woody tissue production, and hence the nature of production in tropical forests.

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AUTHORS' CONTRIBUTIONS

L.R., A.L.D.C., P.M., Y.M. and M.M. designed and implemented the research. P.M. and A.C.L.D. led the experiment and this study. A.L.D.C. and L.R. led recent measurements; all authors contributed to data collection. L.R. analysed the data. L.R. wrote the paper with A.L.D.C., P.M. and M.M., with contributions from all authors.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.qm3gb (Rowland, et al., 2017).

ORCID

Lucy Rowland [iD] http://orcid.org/0000-0002-0774-3216

REFERENCES

Aragão, L. E. O. C., Malhi, Y., Metcalfe, D. B., Silva-Espejo, J. E., Jiménez, E., Navarrete, D., … Anderson, L. O. (2009). Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences*, *6*, 2759–2778. https://doi.org/10.5194/bg-6-2759-2009

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., … Bondeau, A. (2010). Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science*, *329*, 834–838. https://doi.org/10.1126/science.1184984

Bi, J., Knyazikhin, Y., Choi, S. H., & Park, T., Barichivich, J., Ciais, P., … Huete, A. (2015). Sunlight mediated seasonality in canopy structure and photosynthetic activity of Amazonian rainforests. *Environmental Research Letters*, *10*, 064014. https://doi.org/10.1088/1748-9326/10/6/064014

Boisier, J. P., Ciais, P., Ducharne, A., & Guimberteau, M. (2015). Projected strengthening of Amazonian dry season by constrained climate model simulations. *Nature Climate Change*, *5*, 656–660. https://doi.org/10.1038/nclimate2658

Borchert, R., Calle, Z., Strahler, A. H., Baertschi, A., Magill, R., Broadhead, J. S., … Muthuri, C. (2015). Insolation and photoperiodic control of tree development near the equator. *New Phytologist*, *205*, 7–13. https://doi.org/10.1111/nph.12981

Brando, P. M., Nepstad, D. C., Davidson, E. A., Trumbore, S. E., Ray, D., Camargo, P. (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. https://doi.org/10.1098/rstb.2007.0031

Brockwell, P. J., & Davis, R. A. (1991). *Time series: Theory and methods*, (2nd ed.) NewYork, NY: Springer Verlag, pp. 373–375. https://doi.org/10.1007/978-1-4419-0320-4

Cai, W. J., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., … England, M. H. (2014). Increasing frequency of extreme El Nino events due to greenhouse warming. *Nature Climate Change*, *4*, 111–116. https://doi.org/10.1038/nclimate2100

Carswell, F. E., Costa, A. L., Palheta, M., Malhi, Y., Meir, P., Costa, J. D. P. R., … Grace, J. (2002). Seasonality in CO_2 and H_2O flux at an eastern Amazonian rain forest. *Journal of Geophysical Research-Atmospheres*, *107*, LBA 43-1–LBA 43-16.

Chave, J., Navarrete, D., Almeida, S., Alvarez, E., Aragao, L. E. O.C., Bonal, D., Châtelet, P., … Patino, S. (2010). Regional and seasonal patterns of litterfall in tropical South America. *Biogeosciences*, *7*, 43–55. https://doi.org/10.5194/bg-7-43-2010

da Costa, A. C. L., Galbraith, D., Almeida, S., Portela, B. T. T., daCosta, M., de Athaydes Silva Junior, J., … Philips, O. (2010). Effect of 7 year of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist*, *187*, 579–591. https://doi.org/10.1111/j.1469-8137.2010.03309.x

Doughty, C. E., Metcalfe, D. B., Girardin, C. A. J., Amezquita, F. F., Durand, L., Huaraca Huasco, W., … Rocha, W. (2015). Source and sink carbon dynamics and carbon allocation in the Amazon basin. *Global Biogeochemical Cycles*, *29*, 645–655. https://doi.org/10.1002/2014GB005028

Duffy, P. B., Brando, P., Asner, G. P., & Field, C. B. (2015). Projections of future meteorological drought and wet periods in the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 13172–13177. https://doi.org/10.1073/pnas.1421010112

Engelbrecht, B. M. J., Comita, L. S., Condit, R., Kursar, T. A., Tyree, M. T., Turner, B. L., … Hubbell, S. P. (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, *447*, 80–82. https://doi.org/10.1038/nature05747

Feldpausch, T. R., Phillips, O. L., Brienen, R. J. W., Gloor, E., Lloyd, J., Lopez-Gonzalez, G., … Alvarez-Loayza, P. (2016). Amazon forest response to repeated droughts. *Global Biogeochemical Cycles*, *30*, 964–982. https://doi.org/10.1002/2015GB005133

Fisher, R. A., Williams, M., Da Costa, A. L., Malhi, Y., da Costa, R. F., … Meir, P. (2007). The response of an Eastern Amazonian rain forest to drought stress: Results and modelling analyses from a throughfall exclusion experiment. *Global Change Biology*, *13*, 2361–2378. https://doi.org/10.1111/j.1365-2486.2007.01417.x

Fisher, R. A., Williams, M., Ruivo, R. M., Da Costa, A. L., & Meir, P. (2008). Evaluating climatic and soil water controls on evapotranspiration at two Amazonian rainforest sites. *Agriculture and Forest Meteorology*, *148*, 850–861. https://doi.org/10.1016/j.agrformet.2007.12.001

Fu, R., Yin, L., Li, W. H., Arias, P. A., Dickinson, R. E., Huang, L., … Myneni, R. B. (2013). Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 18110–18115. https://doi.org/10.1073/pnas.1302584110

Girardin, C. A. J., Malhi, Y., Doughty, C. E., Metcalfe, D. B., Meir, P., Aguila-Pasquel, J., … Rowland, L. (2016). Seasonal trends of Amazonian

rainforest phenology, net primary productivity, and carbon allocation. *Global Biogeochemical Cycles*, *30*, 700–715. https://doi.org/10.1002/2015GB005270

Hirota, M., Holmgren, M., Van Nes, E. H., & Scheffer, M. (2011). Global resilience of tropical forest and Savanna to critical transitions. *Science*, *334*, 232–235. https://doi.org/10.1126/science.1210657

Körner, C. (2013). Growth controls photosynthesis—mostly. *Nova Acta Leopoldina NF*, *114*, 273–283.

Krepkowski, J., Brauning, A., Gebrekirstos, A., & Strobl, S. (2011). Cambial growth dynamics and climatic control of different tree life forms in tropical mountain forest in Ethiopia. *Trees-Structure and Function*, *25*, 59–70. https://doi.org/10.1007/s00468-010-0460-7

Lenton, T. M. (2011). Early warning of climate tipping points. *Nature Climate Change*, *1*, 201–209. https://doi.org/10.1038/nclimate1143

Lohbeck, M., Lebrija-Trejos, E., Martinez-Ramos, M., Meave, J. A., Poorter, L, & Bongers, F. (2015) Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. *PLoS ONE*, *10*, e0123741. https://doi.org/10.1371/journal.pone.0123741

Makinen, H., Seo, J. W., Nojd, P., Schmitt, U., & Jalkanen, R. (2008). Seasonal dynamics of wood formation: A comparison between pinning, microcoring and dendrometer measurements. *European Journal of Forest Research*, *127*, 235–245. https://doi.org/10.1007/s10342-007-0199-x

Malhi, Y., Aragao, L. E. O. C., Metcalfe, D. B., Paiva, R., Quesada, C. A., Almeida, S., … ANTONIO, C. (2009). Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology*, *15*, 1255–1274. https://doi.org/10.1111/j.1365-2486.2008.01780.x

Malhi, Y., Doughty, C., & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 3225–3245. https://doi.org/10.1098/rstb.2011.0062

Malhi, Y., Doughty, C. E., Goldsmith, G. R., Metcalfe, D. B., Girardin, C. A., Marthews, T. R., … Costa, A. C. (2015). The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. *Global Change Biology*, *21*, 2283–2295. https://doi.org/10.1111/gcb.12859

Marengo, J. A., Tomasella, J., Alves, L. M., Soares, W. R., & Rodriguez, D.A. (2011). The drought of 2010 in the context of historical droughts in the Amazon region. *Geophysical Research Letters*, *38*, L12703. https://doi.org/10.1029/2011gl047436

Meir, P., Wood, T. E., Galbraith, D. R., Brando, P. M., Da Costa, A. C., Rowland, L., … Ferreira, L. V. (2015). Threshold responses to soil moisture deficit by trees and soil in tropical rain forests: Insights from field experiments. *BioScience*, *65*, 882–892. https://doi.org/10.1093/biosci/biv107

Meir, P., & Woodward, F. I. (2010). Amazonian rain forests and drought: Response and vulnerability. *New Phytologist*, *187*, 553–557. https://doi.org/10.1111/j.1469-8137.2010.03390.x

Myneni, R. B., Yang, W. Z., Nemani, R. R., Huete, A. R., Dickinson, R. E., Knyazikhin, Y., … Hashimoto, H. (2007). Large seasonal swings in leaf area of Amazon rainforests. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 4820–4823. https://doi.org/10.1073/pnas.0611338104

Phillips, O. L., van der Heijden, G., Lewis, S. L., Lopez-Gonzalez, G., Aragão, L. E., Lloyd, J., … Amaral, I. (2010). Drought-mortality relationships for tropical forests. *New Phytologist*, *187*, 631–646. https://doi.org/10.1111/j.1469-8137.2010.03359.x

Poorter, L., & Hayashida-Oliver, Y. (2000). Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *Journal of Tropical Ecology*, *16*, 481–498. https://doi.org/10.1017/S026646740000153X

Poorter, L., & Markesteijn, L. (2008). Seedling traits determine drought tolerance of tropical tree species. *Biotropica*, *40*, 321–331. https://doi.org/10.1111/(ISSN)1744-7429

R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rowland, L., da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., Binks, O.J., & Oliveira, A A R., … Ferreira, L. V. (2015). Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature*, *528*, 119–122.

Rowland, L., da Costa, A. C. L., Oliveira, A. A. R., & Almeida, S. S., Ferreira, L. V., … Meir, P. (2017). Data from: Caxiuana monthly litterfall values 2001-2016. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.qm3gb

Rowland, L., Lobo-do-Vale, R. L., Christoffersen, B. O., Melem, E. A., Kruijt, B., Vasconcelos, S. S., … Costa, A. (2015). After more than a decade of soil moisture deficit, tropical rainforest trees maintain photosynthetic capacity, despite increased leaf respiration. *Global Change Biology*, *21*, 4662–4672. https://doi.org/10.1111/gcb.13035

Ruivo, M., & Cunha, E. (2003). Mineral and organic components in archaeological black earth and yellow latosol in Caxiuanã, Amazon, Brazil. In E. Tiezzi, C. A. Brebbia & J. L. Uso (Eds.), *Ecosystems and sustainable development* (pp. 1113–1121). Southampton, UK: WIT Press.

Sakai, S., Harrison, R. D., Momose, K., Kuraji, K., Nagamasu, H., Yasunari, T., … Nakashizuka, T. (2006). Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. *American Journal of Botany*, *93*, 1134–1139. https://doi.org/10.3732/ajb.93.8.1134

Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., … Sugihara, G. (2009). Early-warning signals for critical transitions. *Nature*, *461*, 53–59. https://doi.org/10.1038/nature08227

Wagner, F. H., Herault, B., Bonal, D., Stahl, C., Anderson, L. O., Baker, T. R., … Bowman, D. M. (2016). Climate seasonality limits leaf carbon assimilation and wood productivity in tropical forests. *Biogeosciences*, *13*, 2537–2562. https://doi.org/10.5194/bg-13-2537-2016

Wright, S. J., & Cornejo, F. H. (1990). Seasonal drought and leaf fall in a tropical forest. *Ecology*, *71*, 1165–1175. https://doi.org/10.2307/1937384

Wu, J., Albert, L. P., Lopes, A. P., Restrepo-Coupe, N., Hayek, M., Wiedemann, K. T., … Tavares, J. V. (2016). Leaf development and demography explain photosynthetic seasonality in Amazon evergreen forests. *Science*, *351*, 972–976. https://doi.org/10.1126/science.aad5068

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