Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest

Antonio Carlos Lola da Costa[1], David Galbraith[2,3], Samuel Almeida[4], Bruno Takeshi Tanaka Portela[1], Mauricio da Costa[1], João de Athaydes Silva Junior[1], Alan P. Braga[1], Paulo H. L. de Gonçalves[1], Alex AR de Oliveira[1], Rosie Fisher[5], Oliver L. Phillips[6], Daniel B. Metcalfe[7], Peter Levy[3] and Patrick Meir[2]

[1]Universidade Federal do Pará, Centro de Geociências, Belém, CEP 66017-970, Pará, Brazil; [2]School of Geosciences, University of Edinburgh, Drummond Street, Edinburgh, EH8 9XP; [3]Centre for Ecology and Hydrology, Edinburgh, Bush Estate, Penicuik, Midlothian, EH26 0QB, UK; [4]Museu Paraense Emilio Goeldi, Coordenação de Botânica, Belém, CEP 66077-530, Pará, Brazil; [5]Los Alamos National Laboratory, Los Alamos, NM 87545, USA; [6]Ecology and Global Change, School of Geography, University of Leeds, Leeds, LS2 9JT, UK; [7]Centre for the Environment, University of Oxford, Oxford, OX1 3QY, UK

Summary

- At least one climate model predicts severe reductions of rainfall over Amazonia during this century. Long-term throughfall exclusion (TFE) experiments represent the best available means to investigate the resilience of the Amazon rainforest to such droughts.
- Results are presented from a 7 yr TFE study at Caxiuanã National Forest, eastern Amazonia. We focus on the impacts of the drought on tree mortality, wood production and above-ground biomass.
- Tree mortality in the TFE plot over the experimental period was 2.5% yr^{-1}, compared with 1.25% yr^{-1} in a nearby control plot experiencing normal rainfall. Differences in stem mortality between plots were greatest in the largest (> 40 cm diameter at breast height (dbh)) size class (4.1% yr^{-1} in the TFE and 1.4% yr^{-1} in the control). Wood production in the TFE plot was *c.* 30% lower than in the control plot. Together, these changes resulted in a loss of 37.8 ± 2.0 Mg carbon (C) ha^{-1} in the TFE plot (2002–2008), compared with no change in the control.
- These results are remarkably consistent with those from another TFE (at Tapajós National Forest), suggesting that eastern Amazonian forests may respond to prolonged drought in a predictable manner.

Introduction

The Amazon rainforest stores 70–120 Pg of carbon (C) in its vegetation (Houghton *et al.*, 2001; Malhi *et al.*, 2006; Saatchi *et al.*, 2007) and possesses exceptional, but poorly quantified, species richness (Hopkins, 2007). Drought has the potential both to reduce above-ground biomass storage (Rolim *et al.*, 2005) and, in the longer term, alter forest composition (Engelbrecht *et al.*, 2007). The Amazon rainforest has been hit by punctuated drought events on a number of occasions over the last 100 yr (Sombroek, 2001), including the El Niño-Southern Oscillation (ENSO) events of 1983

and 1997–1998, centred on Manaus and eastern Amazonia, and the 2005 drought, centred over western Amazonia. Such droughts have had a significant impact on forest structure, resulting in increased occurrence of forest fires (Alencar *et al.*, 2006; Aragão *et al.*, 2008) and higher tree mortality (Williamson *et al.*, 2000; Laurance & Williamson, 2001; Phillips *et al.*, 2009). In fact, Phillips *et al.* (2009) report that the losses of biomass resulting from increased mortality and reduced growth during the 2005 drought were sufficient to 'switch off' the pre-existing pan-Amazonian above-ground carbon sink. Several studies in other tropical rainforest sites generally confirm the pattern

of increased mortality following droughts associated with ENSO events (Leighton & Wirawan, 1984; Nakagawa *et al.*, 2000; Van Nieuwstadt & Sheil, 2005; but see Condit *et al.*, 1995 and Aiba & Kitayama, 2002). Such episodic drought events are generally short-lived, with recovery of mortality rates to background rates ensuing relatively quickly (Williamson *et al.*, 2000).

However, at least one climate model (Cox *et al.*, 2000; Betts *et al.*, 2004) predicts large (up to 50%), persistent reductions in rainfall over Amazonia by the end of this century, although climate model predictions vary widely (Li *et al.*, 2006; Malhi *et al.*, 2009a). Large-scale deforestation, too, could result in reduced precipitation over Amazonia (Costa & Foley, 2000; Hoffmann *et al.*, 2003). Although studies focusing on isolated natural drought events are important for understanding short-term responses of rainforest to drought, it is unclear how much insight they provide into the response of Amazonian rainforests to the longer-term, sustained reductions in rainfall projected by future climate/land-use scenarios. However, throughfall exclusion (TFE) experiments, where a percentage of total canopy throughfall is prevented from reaching the soil by means of large plastic panels just above ground level, have been specifically designed to investigate the response by forest ecosystems to longer-term drought. Two such experiments, described comprehensively in Meir *et al.* (2009), have been installed in eastern Amazonia (in Tapajós National Forest and Caxiuanã National Forest), where the most severe reductions in rainfall in the region are predicted by some climate models (Malhi *et al.*, 2009a).

Stem growth and mortality are the two major fluxes determining above-ground biomass. At the Tapajós TFE, Nepstad *et al.* (2007) reported significant increases in stem mortality following 3 yr of throughfall exclusion, particularly in large trees, where stem mortality rates increased 4.5-fold. Reductions in wood production of up to 60% yr^{-1} were also reported at the same site (Brando *et al.*, 2008). However, in the absence of suitable data from elsewhere, it remains unclear how representative these results are of eastern Amazonian rainforests as a whole. Here we present results from 8 yr (1 yr pretreatment and 7 yr of TFE treatment) of mortality and growth data collected at a separate Amazonian TFE study, located in Caxiuanã National Forest, state of Pará, Brazil. The experimental design of the study was similar to that of the Tapajós TFE (Nepstad *et al.*, 2002), whereby *c.* 50% of the incident rainfall was channelled outside of the study area and consequently prevented from reaching the soil (Fisher *et al.*, 2007), but the reporting period for this experimental manipulation is longer. Of particular interest is whether a consistent pattern emerges across both TFE experiments and whether the results are consistent with the shorter-term (1 yr), but spatially extensive, analysis of the 2005 drought in Amazonia reported by Phillips *et al.* (2009). Such information is critical for constraining predictions of dynamic global vegetation models (DGVMs), which vary widely in the simulated sensitivity of the Amazon forest to drought stress (Ostle *et al.*, 2009; Galbraith *et al.*, 2010).

Also, of substantial importance, is the possible impact of drought on forest species composition (Engelbrecht *et al.*, 2007; Meir *et al.*, 2009). Rainfall has been shown to be a strong predictor of maximum tree alpha-diversity in Amazonia (ter Steege *et al.*, 2003), with wetter forests exhibiting higher species richness (Butt *et al.*, 2008). Moisture limitation has also been invoked as the cause of reduced species richness over a 10 yr period in French Guiana (Fonty *et al.*, 2009). We looked for evidence of differential responses of tree taxa to drought and compared these with published data from the Tapajós TFE (Nepstad *et al.*, 2007, appendix). Consistent differences in responses to drought among tree taxa would indicate that long-term compositional shifts are very likely.

In short, we address the following questions: first, what is the impact of 7 yr of throughfall exclusion on tree mortality, recruitment and wood production; second, how do changes in stem mortality, recruitment and wood production affect above-ground woody biomass stocks; and third, are there differences in responses to drought across different taxa and different size classes?

Materials and Methods

Site description and experimental design

The experimental site is located in Caxiuanã National Forest Reserve in the eastern Brazilian Amazon (1°43′S, 51°27′W) and is administered by the Estação Científica Ferreira Penna (ECFPn) which belongs to the Museu Paraense Emílio Goeldi (MPEG). It is a *terra firme* forest that has been a reserve since the 1970s, is extensive (33 000 ha) and is largely undisturbed (Lisboa & Ferraz, 1999; Carswell *et al.*, 2002). Mean annual rainfall is between 2000 and 2500 mm, with a pronounced dry season between June and November. The soil is a yellow oxisol (Brazilian classification *latossolo amarelo*) with a thick stony/laterite layer at 3–4 m depth. Soil texture is 75–83% sand, 12–19% clay and 6–10% silt (Ruivo & Cunha, 2003). The site elevation is 15 m above river level in the dry season and the water table has been occasionally observed at a soil depth of 10 m during the wet season.

From January 2002, *c.* 50% of the incident rainfall was excluded from a 1 ha treatment plot (hereinafter referred to as the TFE plot) using a system of plastic panels and plastic-lined guttering installed at a height of 1–2 m (Fisher *et al.*, 2007; Meir *et al.*, 2009). The covering was in place continuously over the time-frame of this study (January 2002–December 2008), except for a 1 wk period in November of 2002 (full removal) and during 2004 (*c.* 30% removal).

The effect of throughfall exclusion on the TFE plot was assessed relative to a 1 ha control plot located nearby (< 50 m from the TFE plot) and relative to measurements made in the TFE plot before the installation of the experiment (between September 2000 and December 2001). Trenches (1–2 m deep) were dug around the perimeters of both plots to reduce the lateral inflow of water through the soil matrix from outside the plots. Both plots were subdivided into 100 subplots of 10 m × 10 m each. To control for any impact from the trenching process, trees occurring in the subplots closest to the trenches were excluded from the analysis. Thus, the effective plot size considered in the analysis was 0.64 ha.

The treatment could not be replicated because of logistical and financial constraints, but the method follows the design of other unreplicated large-scale ecosystem manipulation experiments (e.g. Likens *et al.*, 1970), whose strength is acknowledged, especially where large treatment effects are expected (Hurlbert, 2004). An additional key feature of our study is that we further strengthen our analysis through comparison of the mortality and growth rates in the TFE plot with those from a series of local plots (eight in total, all < 50 km from the study site, all in the Caxiuanã National Forest Reserve), as well as with the control plot. Although this multiplot comparison cannot directly substitute for full experimental replication at the necessary large scale of the experimental treatment, it serves to place our measurements in the context of the background variability in forest growth dynamics, greatly strengthening our understanding of the generality of the impact of the TFE treatment on eastern Amazonian rainforests.

Rainfall and soil moisture data

Meteorological data (rainfall, air temperature, atmospheric humidity, solar radiation, wind speed) was collected at half-hourly resolution using an automatic weather station located at the top (51.5 m) of a tower 1 km from the experimental plot. Rainfall was measured using a tipping bucket rainfall gauge (CS700-L; Campbell Scientific, Loughborough, UK) with a resolution of 0.2 mm. Four soil access pits were constructed in each plot to measure soil moisture up to a depth of 5 m, using time domain reflectometry (TDR) sensors, as described by Fisher *et al.* (2007). High-quality soil moisture data were only available for the period from January 2001 to April 2004. These data are published in Fisher *et al.* (2007). Here, the soil–plant–atmosphere (SPA) model (Williams *et al.*, 1996; with site-specific soil and vegetation parameterizations, as applied in Fisher *et al.*, 2007), was driven with the half-hourly meteorological data to simulate soil moisture during the entire time-frame of the experiment. SPA predictions of soil moisture at Caxiuanã have previously been found to provide excellent (R^2 = 0.87) agreement with field measurements during the first 2 yr (2002–2003) of exclusion (Fisher *et al.*, 2007).

Tree growth, recruitment and mortality

An initial inventory of stems ≥ 10 cm diameter at breast height (dbh) was conducted in September 2000, during which trees were identified to species level and dbh was measured. Diameters were measured at 1.3 m (dbh), except in the case of buttressed stems, which were measured above the buttress to avoid overestimation (Condit, 1998). Individuals present in the initial inventory were re-censused on several occasions throughout the experiment, at varying census intervals, up to December 2008. During each census, each tree was assessed as either being alive or dead and the increment in stem circumference was measured using dendrometer bands (Metcalfe *et al.*, 2009). Recruitment of new individuals not included in the initial inventory was carried out in August 2005. For analysis, trees were grouped into three size classes, based on dbh at the beginning of the experiment: 'small' trees (10–20 cm dbh); 'medium' trees (20–40 cm dbh); and 'large' trees (> 40 cm dbh). When used throughout this document, the terms 'small', 'medium' and 'large' refer specifically to these categories.

Mortality was assessed as death or disappearance of previously permanently marked stems (Metcalfe *et al.*, 2009). Mortality rates were calculated according to Sheil & May (1996), as in Nepstad *et al.* (2007):

$$m = \left\lfloor 1 - (1 - S_{D}/N_0)^{1/t} \right\rfloor \qquad \text{Eqn 1}$$

where N_0 is the number of stems present at the beginning of the interval, S_D is the number of stems that died during the interval and t is the duration of the interval in yr. Measurement intervals varied during the experiment from 1 to 13 months, so for analysis, measurement intervals of short duration (1–6 months) were grouped together into intervals of *c*. 1 yr. Mortality rates of the control and TFE plots were further compared with those of eight other census plots located nearby.

Recruitment rates (r) into individual diameter size classes were also calculated as in Nepstad *et al.* (2007):

$$r = \left\lfloor (1 + X/N)^{1/t} - 1 \right\rfloor \qquad \text{Eqn 2}$$

where X is the number of stems growing into the diameter class during the census interval and N and t are as defined in Eqn 1.

Increments in stem circumference (Δc) measured by the dendrometer bands were converted into diameter growth increments (Δdbh) (Δdbh = $\Delta c/\pi$) and grouped into 1 yr intervals for further analysis. The same diameter size classes

used in the mortality and recruitment data were used in the analysis of diameter growth data.

Biomass calculations

Allometric equations represent an acknowledged key source of uncertainty in above-ground biomass estimates (Chave *et al.*, 2004; Keller *et al.*, 2001; Nogueira *et al.*, 2008). As there have been no allometric equations developed specifically for the Caxiuanã, we use eight previously published allometric equations to calculate the initial standing above-ground biomass (in kg dry mass) in both plots and also changes in biomass as a result of stem growth and mortality. We estimated a mean and 95% confidence intervals from the biomass values produced by these equations (Table 1). For six of the eight equations used, only information on dbh is required. The allometric equations derived by Baker *et al.* (2004) and Chave *et al.* (2005) require information on wood density, which was obtained from Baker *et al.* (2004), Fearnside (1997) and from the Global Wood Density Database (Zanne *et al.*, 2009, available online at http://datadryad.org/repo/handle/10255/dryad.235).

Differential responses of tree genera

As the number of individuals belonging to a given species was relatively low, we looked for differences in the drought treatment across tree genera. While we acknowledge that in some cases different species within a genus can vary in their vulnerability to drought (Abrams, 1990), this step was necessary to increase the sample size for our data analysis, and is a procedure that is employed elsewhere (Butt *et al.*, 2008; van Mantgem *et al.*, 2009). We focused our analysis on genera that were represented by at least eight individuals (> 10 cm dbh) in the TFE plot. We compared the

mortality and growth of these genera (13 in total) in the TFE plot with their equivalent rates in the control plot. We also compared our genus-specific mortality values with those in the Tapajós TFE, as provided in the appendix of Nepstad *et al.* (2007).

Statistical analysis

To analyse the mortality data, we followed the same statistical procedure employed in Nepstad *et al.* (2007), in which a 2×2 contingency table analysis is used to examine differences in mortality between plots (TFE, control and other local Caxiuanã plots). Table cells contained the number of trees present at the start of the census interval and the number of trees that died during the census interval. The statistical significance of the difference in mortality rates between plots was assessed using Fisher's exact test. This analysis was repeated for all size classes and for all census intervals. The low number of trees per genus precluded an in-depth statistical analysis of genus-specific responses to drought. As small differences between plots could be the result of sampling error, we considered genus-specific differences between plots to signify high vulnerability to drought if mortality rates were at least 50% (1.5-fold) and at least two individuals greater in the TFE than in the control plot.

Results

Rainfall and soil moisture

Average annual rainfall during the study period was 2231 ± 75 mm yr^{-1}. Average dry season (June–November) rainfall was 536 ± 88 mm yr^{-1} and thus accounted for less than a quarter of total annual rainfall. Variability in dry season rainfall across years was also much greater than

Table 1 Allometric equations used to calculate above-ground biomass *M* (kg) for all trees > 10 cm diameter at breast height (dbh)

Equation	a	b	c	d	Reference
$M = a + bD + cD^2$	42.69	−12.8	1.242	–	Brown (1997)
$M = \exp(a + b \log_e(D))$	−2.134	2.53	–	–	Brown (1997)
$M = 0.57 \exp(a + b \log_e(D))$	−1.754 (trees < 20 cm dbh); −0.151 (trees ≥ 20 cm dbh)	2.665 (trees < 20 cm dbh); 2.17 (trees ≥ 20 cm dbh)	–	–	Higuchi *et al.* (1998)
$M = 1000a \exp(b + c \log_e(D/100))$	0.6	3.323	2.546	–	Carvalho *et al.* (1998)
$M = a(bD^c)$	0.6	4.06	1.76	–	Araújo *et al.* (1999)
$M = \exp(a + b \log_e(D) + c(\log_e(D))^2 + d(\log_e(D))^3)$	−0.37	0.333	0.933	−0.122	Chambers *et al.* (2001)
$M = (\rho/0.67)\exp(a + b \log_e(D) + c(\log_e(D))^2 + d(\log_e(D))^3)$	−0.37	0.333	0.933	−0.122	Baker *et al.* (2004)
$M = \rho \exp(a + b \log_e(D) + c(\log_e(D))^2 + d(\log_e(D))^3)$	−1.499	2.148	0.207	−0.0281	Chave *et al.* (2005)

D, diameter at breast height (cm); ρ, wood density (g cm^{-3}). The original Higuchi *et al.* (1998) equation provides biomass estimates in fresh mass; we multiply by 0.57 to estimate oven-dry mass, following Nogueira *et al.* (2008). *a*, *b*, *c*, *d* are empirical parameters of the allometric equations.

variability in annual rainfall (Fig. 1). Dry season rainfall ranged from a low of 340 mm in 2005 to a high of 714 mm in 2001. Commencement of the drought experiment in January 2002 led to immediate reductions in soil moisture content in the TFE plot that were maintained throughout the remainder of the experiment (Fig. 1). Over the exclusion period, daily modelled soil moisture content (top 10 m) in the control plot ranged from 2171 mm (December 2004) to 3178 mm (April 2008). In the TFE plot, average daily modelled soil moisture content (top 10 m) over the exclusion period ranged from 2098 mm (December 2004) to 2618 mm (June 2008). Average annual modelled soil moisture values in both plots were lowest in 2005 (2560 ± 26 mm in the control plot and 2255 ± 11 mm in the TFE plot). Over the entire duration of the exclusion, modelled soil moisture in the TFE plot was 388 ± 14 mm lower than in the control in the wet season and 252 ± 40 mm lower in the dry season.

Initial inventory

At the beginning of the experiment, both control and TFE plots were broadly similar in terms of their distribution of diameter size classes and biomass content. Many of the tree species occurred in both plots, although there were

differences in their relative abundances. In the first inventory in September 2000, the control plot contained 534 trees above 10 cm dbh while the TFE plot contained 501 trees above 10 cm dbh. The most dominant species, in terms of number of individuals, in the control plot were *Rinorea guianensis*, *Vouacapoua americana* and *Pouteria decorticans*, while the dominant species in the TFE plot were *Eschweilera coriacea*, *Tetragastris panamensis* and *Manilkara bidentata*. In the control plot, 56% of the trees in the initial census interval were between 10 and 20 cm dbh, 33% were between 20 and 40 cm dbh, and 11% had a dbh of over 40 cm. This was very similar to the TFE plot, for which the values were 58, 30 and 12%, respectively. Total above-ground biomass of inventoried trees was estimated to be 213.9 ± 14.2 Mg C ha^{-1} in the control plot and 200.6 ± 13.2 Mg C ha^{-1} in the TFE plot. These values are similar to estimates of above-ground biomass reported in other measurement plots in the Caxiuanã National Forest (Malhi *et al.*, 2009b).

Stem mortality rates

Recruitment rates were only assessed at one point during the study (December 2005) and were found to be similar in both plots, averaging 0.9% yr^{-1} in the control plot and
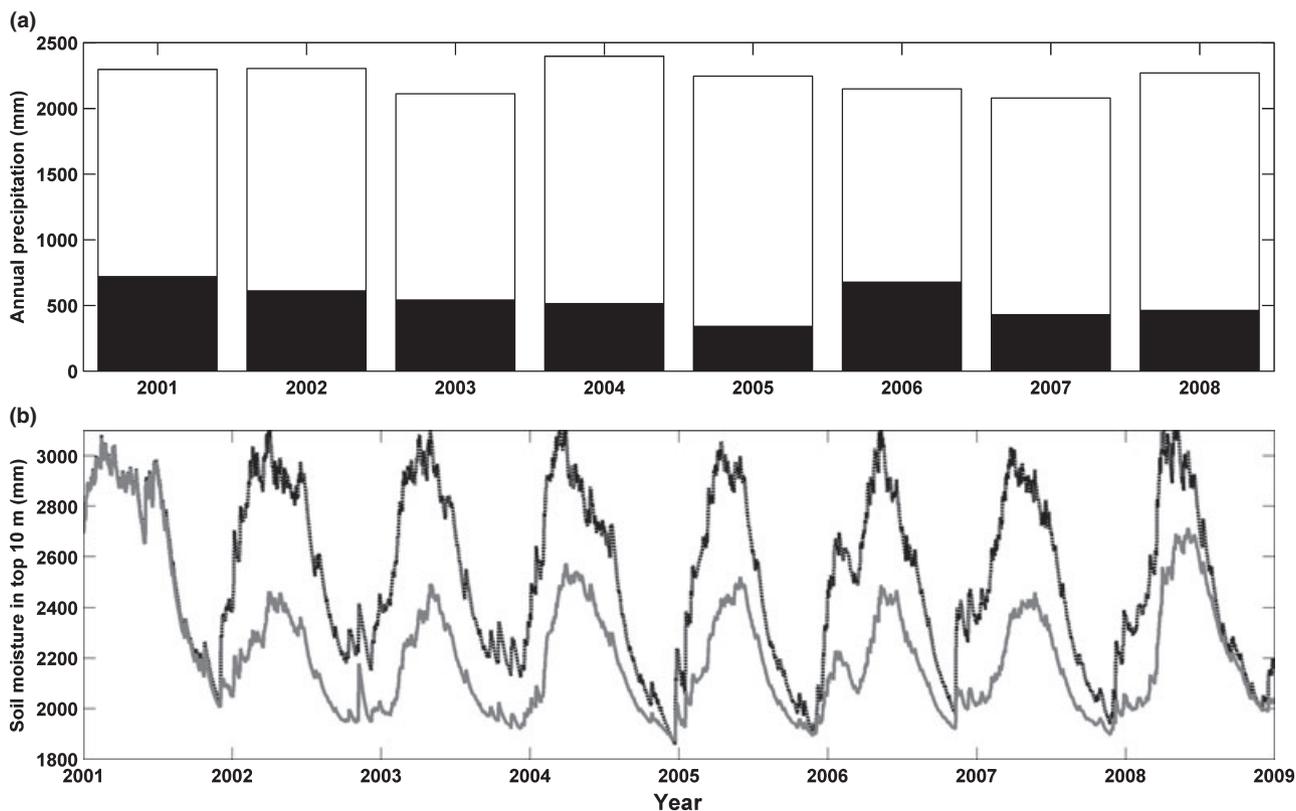

Fig. 1 (a) Annual rainfall during 2001–2008. Black bars, dry season; white bars, wet season. (b) Daily soil moisture content to 10 m simulated with the soil–plant–atmosphere (SPA) model. Black line, control; grey line, throughfall exclusion (TFE). The exclusion of rainfall in the TFE plot began in January 2002.

1.05% yr^{-1} in the TFE plot for all trees > 10 cm dbh (Fig. 2a). This amounts to *c*. 5 newly recruited trees > 10 cm dbh in each plot per year. Pre-experiment (2001) stem mortality rate in both plots was *c*. 0.5% yr^{-1} (Fig. 3), which is below the longer-term (8 yr) mean of the control plot (1.2% yr^{-1}), but is within the range of annual mortality rates of other Caxiuanã plots (0.5–1.7% yr^{-1}). However, large differences in annual mortality rates were observed between plots over the exclusion period (January 2002–December 2008; Fig. 2). Across all size classes, the annual mortality rate in the TFE plot was approximately

double that of the control plot (2.5% yr^{-1}, compared with 1.25% yr^{-1}). For the period where both recruitment and mortality data were available (September 2000–December 2005), recruitment rates in the control plot exceeded mortality rates for small and medium trees, but not large trees. In the TFE plot, stem mortality exceeded recruitment in all size classes (Fig. 2). Considerable variability was observed in annual mortality in both plots (Fig. 3), but the difference between plots was much more accentuated and only statistically significant (Fisher's exact test, $P < 0.01$) in the second half of the experiment. A peak in mortality rates
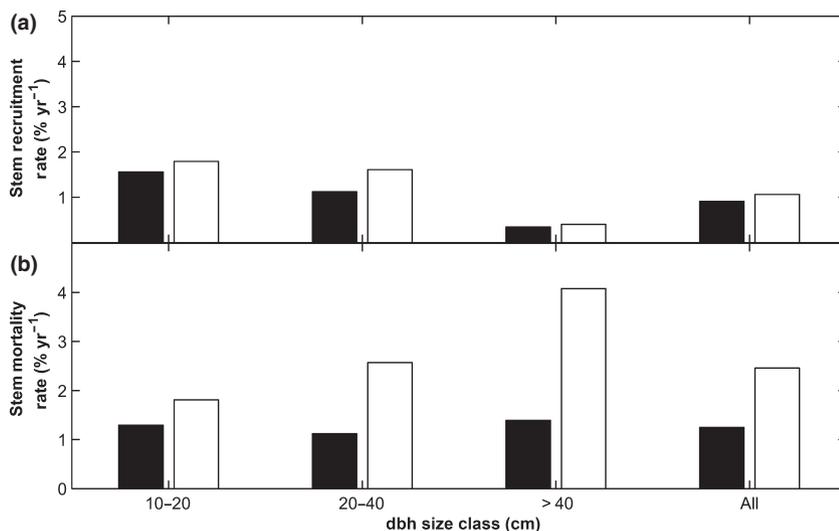

Fig. 2 Summary of annual recruitment (a) and annual mortality rates (b) in the control (black bars) and throughfall exclusion (TFE, white bars) plots. Annual mortality rates are presented as the mean during the exclusion period (January 2002–December 2008) while recruitment rates are the mean of the period from September 2000 to December 2005. dbh, diameter at breast height.
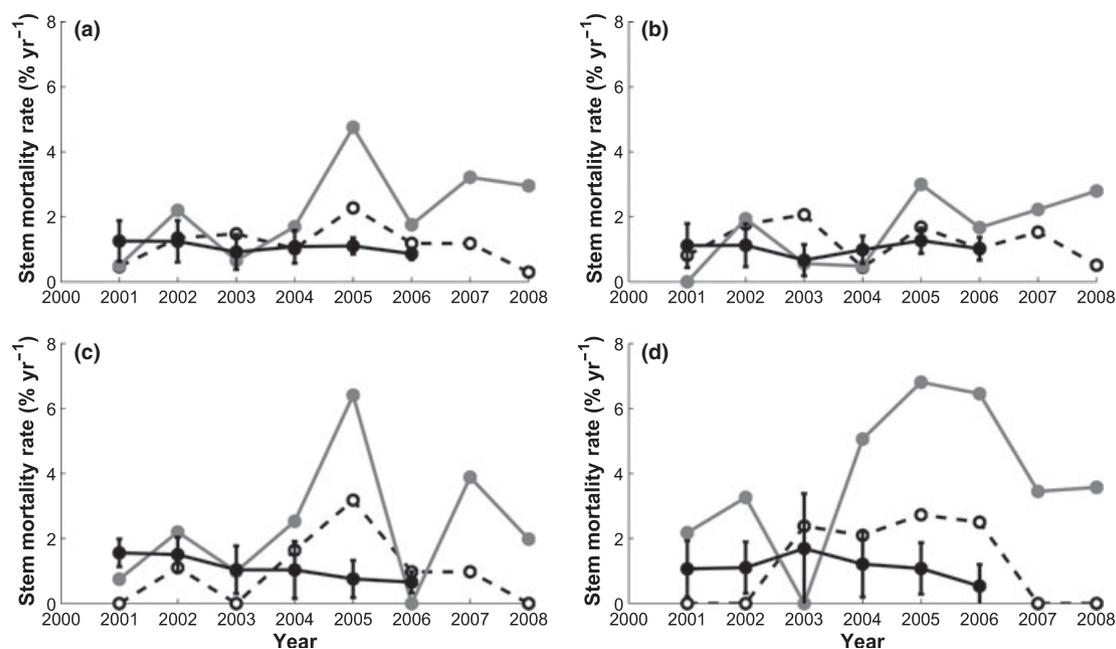

Fig. 3 Annual stem mortality rates during the study period (2001–2008). Other measurement plots are nearby sites (*n* ranges annually from 2 to 7) which are censused on a quasi-annual basis, but were not part of the experiment. (a) All trees; (b) diameter at breast height (dbh) 10–20 cm; (c) dbh 20–40 cm; (d) dbh > 40 cm. Open circles, control plot; grey circles, throughfall exclusion (TFE) plot; closed circles, other measurement plots.

occurred in both plots in 2005. During this peak, annual mortality across all trees reached 4.8% yr^{-1} in the TFE plot and 2.3% yr^{-1} in the control plot. This peak coincided with the year of the most severe dry season over the study period (Fig. 1), where rainfall in June to November was only 340 mm, compared with a mean of 565 ± 80 mm across other years. Annual mortality in the control plot was slightly higher, but not statistically different from that of other Caxiuanã plots, whereas mortality rates in the TFE plot were statistically higher than those of other nearby plots in the latter half of the experiment (Fisher's exact test, $P < 0.01$; Fig. 3a).

The smallest difference in mortality between the TFE and control plots was found for small trees, where average mortality rates over the exclusion period were 1.2% yr^{-1} in the control plot and 1.8% yr^{-1} (Fisher's exact test, $P = 0.09$) in the TFE plot (Fig. 3b). Mortality rate of medium trees was 1.1% yr^{-1} for the control plot and 2.6% yr^{-1} for the TFE plot (Fisher's exact test, $P = 0.17$; Fig. 3c). The biggest differences in mortality rates were observed in the large size class where annual mortality rate over the exclusion period was 1.4% yr^{-1} in the control plot and 4.1% yr^{-1} in the TFE plot (Fisher's exact test, $P = 0.03$; Fig. 3d). Large trees exhibited the greatest variability in mortality rates of all size classes (Fig. 3d). For example, mortality rates of large trees in the TFE plot ranged from 0.0 to 6.8% yr^{-1} during the study period. These oscillations in annual mortality rates are not surprising, as there are fewer large trees (c. 50 per plot) than those in other size categories.

Wood production

Above-ground wood production before the exclusion period was very similar between plots, but over the exclusion period it was on average 32% lower in the TFE plot (1.32 ± 0.11 Mg C ha^{-1} yr^{-1}) than in the control plot (1.94 ± 0.22 Mg C ha^{-1} yr^{-1}), with maximum difference

in 2007 when the difference between plots increased to c. 50% (Fig. 4). Above-ground wood production was higher in the control plot than in the TFE plot across all years, except for 2002. Almost all of the difference in wood production between the TFE and control plots was accounted for by the reduction in wood production of large trees in the TFE plot. Over the exclusion period, wood production in the largest size class in the TFE plot was only 35% of that of the control plot (0.39 ± 0.05 Mg C ha^{-1} yr^{-1} vs 0.92 ± 0.21 Mg C ha^{-1} yr^{-1}). Large trees accounted for 47% (compared with 55% in the pre-exclusion period) of the above-ground productivity during the exclusion period in the control plot but for only 29% (compared with 39% in the pre-exclusion period) of the above-ground productivity over the same period in the TFE plot (Fig. 4). The difference in the wood production of large trees was a result of both a reduction in the density of large trees and a reduction in the average growth rate of large trees. The average diameter growth rate of large trees in the TFE plot over the exclusion period was 0.91 ± 1.06 mm yr^{-1} compared with 2.01 ± 1.05 mm yr^{-1}. Wood production of medium trees was also reduced in the TFE plot relative to the control plot over the exclusion period (0.56 ± 0.10 vs 0.71 ± 0.06 Mg C ha^{-1} C yr^{-1}). The drought treatment appeared to have little effect on the wood production of small trees, which was slightly greater in the TFE plot than in the control plot over the exclusion period (0.36 ± 0.05 vs 0.30 ± 0.05 Mg C ha^{-1} C yr^{-1}).

Net biomass impacts

In the TFE plot, a total of 48.1 ± 3.4 Mg C ha^{-1} (6.6 Mg C ha^{-1} yr^{-1}) of above-ground biomass was lost through tree mortality over the 7 yr exclusion period, compared with 14.7 ± 0.8 Mg C (1.8 Mg C ha^{-1} yr^{-1}) in the control plot. Thus, tree mortality led to 227% more dead matter in the TFE plot than in the control plot. Large trees

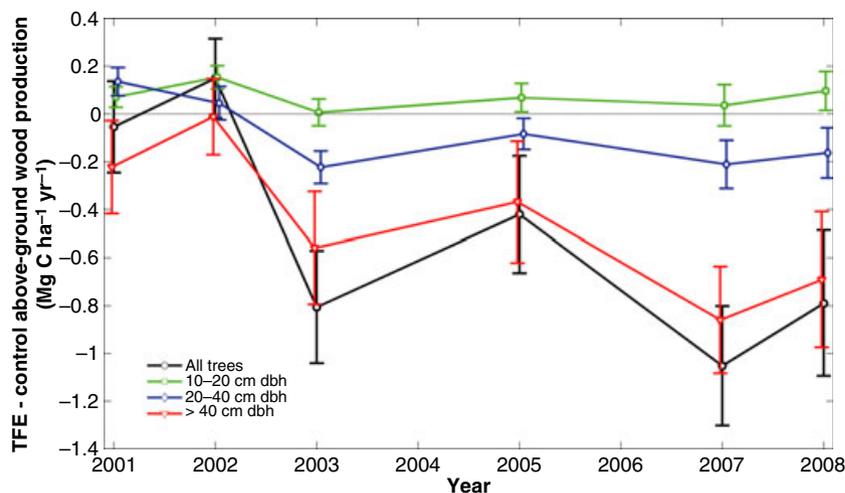**Fig. 4** Difference in above-ground wood production (Mg C ha^{-1} yr^{-1}) between the throughfall exclusion (TFE) and control plots (i.e. TFE – control). Data are normalized to account for initial differences in biomass between plots. Error bars, 95% confidence intervals, derived from biomass estimates from eight different allometric equations.
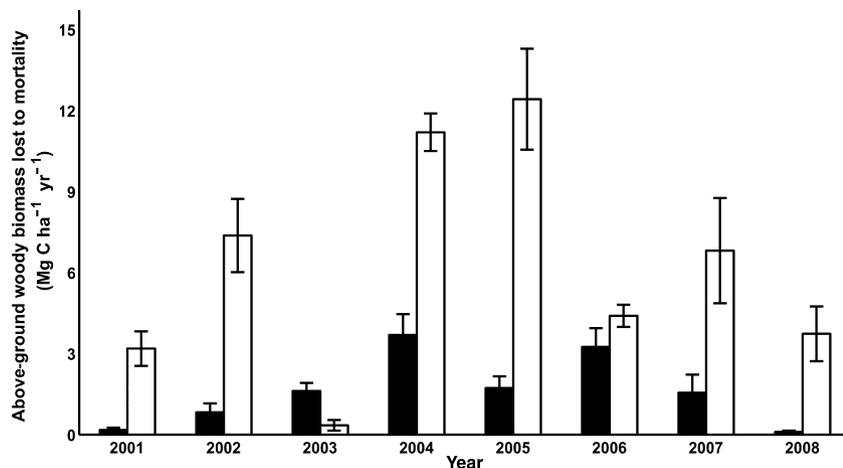
Fig. 5 Annual variation in biomass lost to mortality in the throughfall exclusion (TFE, open bars) and control (closed bars) plots. Error bars, 95% confidence intervals, derived from biomass estimates from eight different allometric equations.
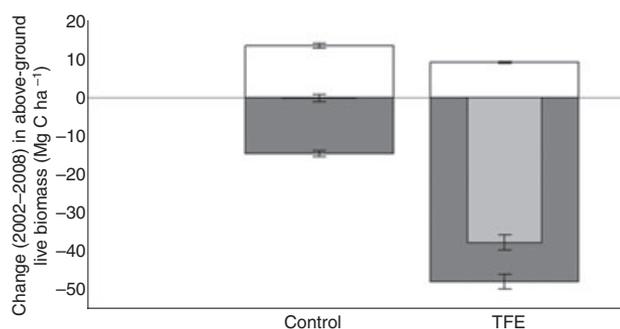

Fig. 6 Change in above-ground woody biomass (Mg C ha^{-1}) of trees > 10 cm diameter at breast height (dbh) over the exclusion period (2002–2008). Error bars, 95% confidence intervals, derived from biomass estimates from eight different allometric equations. TFE, throughfall exclusion; white boxes, growth and recruitment; dark grey boxes, mortality; light grey box, net change.

accounted for 79% of the total biomass lost to mortality in the TFE plot and for 55% of the total in the control plot. Year-to-year variability was relatively high in annual biomass losses to mortality, and was heavily skewed by the death of very large trees (Fig. 5). The net effect of all above-ground biomass fluxes (including a small recruitment term) was close to zero in the control plot (Fig. 6). This change in biomass is comparable to that observed in the other local plots in Caxiuanã (0.34 ± 0.35 Mg C ha^{-1} yr^{-1}). In the TFE plot, however, standing biomass decreased by 37.8 ± 2.0 Mg C ha^{-1} (5.4 Mg C ha^{-1} yr^{-1}). Thus, the net effect was an approximate loss of 18–20% in the TFE plot over the 7 yr exclusion period, compared with no change in the control plot.

Taxonomic effects

The mortality rates of the 13 most common tree genera in the TFE plot are shown in Table 2 and compared, where possible, with the same genera in the control plot. Using the criteria outlined in the Materials and Methods section,

we found evidence of high vulnerability to drought for three genera (*Eschweilera*, *Inga* and *Manilkara*) in the TFE plot relative to the control plot. Five genera (*Licania*, *Minquartia*, *Protium*, *Swartzia* and *Pouteria*) showed no obvious evidence of high vulnerability to drought (according to the criteria outlined in the Materials and Methods section). *Micropholis*, *Ouratea* and *Xylopia* showed high mortality in the TFE plot (37.5, 18.2 and 37.5%) but the sample sizes for these genera in the control plot were too low for direct comparison.

Discussion

Drought-induced mortality

The drought treatment led to a striking reduction in above-ground standing biomass. While above-ground woody biomass in the control plot was virtually unchanged over the exclusion period, the TFE plot lost *c.* 20% of its above-ground biomass, mainly because of large increases in mortality of large trees (Figs 5, 6). Indeed, the overall mortality in the TFE plot was approximately double that of the control plot over the exclusion period. Despite some intercensus variability, there was a clear trend of increasing mortality in the TFE plot as the drought progressed. During the first 3 yr of the exclusion period (2002–2004), stem mortality in the TFE plot was 1.5% yr^{-1} compared with 1.25% yr^{-1} in the control plot. However, during the last 4 yr of the exclusion period (2005–2008), the mortality rate in the TFE plot averaged 3.2% yr^{-1} compared with 1.15% yr^{-1} in the control plot. Thus, mortality in the TFE plot over the latter half of the exclusion period was almost three times higher than the control plot over the same period and more than double the mortality in the TFE plot in the first half of the exclusion period.

Mortality rates can vary considerably in space and time (e.g. Lewis *et al.*, 2004). However, we gain additional confidence that the observed treatment effects on mortality

Table 2 Mortality rates (2002–2008) of genera represented by eight or more individuals in the throughfall exclusion (TFE) plot and their equivalent mortality in the control plot

Genus	Main species	n (control)	n dead (control)	Mortality (%, control)	n (TFE)	n dead (TFE)	Mortality (%, TFE)
Genera with ≥ eight individuals in both plots							
Eschweilera	E. coreacea, E. grandiflora	16	0	0	17	3	**17.7**
Inga	I. alba, I. gracilifolia	9	0	0	12	3	**25.0**
Licania	L. heteromorpha L. octandra	29	2	6.9	19	1	5.3
Manilkara	M. bidentata, M. paraensis	12	0	0	14	3	**21.4**
Minquartia	M. guianensis	8	2	25.0	9	0	0
Pouteria	P. cladantha, P. decorticans, P. guianensis	44	3	6.9	30	3	10.0
Protium	P. tenuifolium, P. Trifoliolatum	16	1	6.3	13	2	15.4
Swartzia	S. brachyracchis, S. racemosum	15	3	20.0	8	1	12.5
Genera with ≥ eight individuals in the TFE plot but not in the control							
Lecythis	L. confertiflora, L. idatimon	3	0	0	17	1	5.9
Micropholis	M. venulosa	6	1	16.7	8	3	37.5
Ouratea	O. leprieuri	2	0	0	11	2	18.2
Stachyarrhena	S. spicata	4	0	0	9	1	11.1
Tetragastris	T. panamensis	4	1	25.0	13	1	7.7
Xylopia	X.nitida	0	0	0	8	3	37.5

Bold type refers to mortality increases in the TFE plot that may signify vulnerability of that genus to drought, as they are 1.5-fold and at least two individuals greater than the control plot.

are real, as mortality rates in the latter half of the TFE treatment (2005–2008) greatly exceeded the mortality rates reported in the other local nonexperimental plots ($n = 8$) during the period where census data were available for these plots (2001–2006; Fig. 3). These additional treatment plots provide an important local context which is often missing for unreplicated large-scale manipulation experiments.

There is a remarkable consistency between our mortality results and those reported from the Tapajós TFE. First, mortality rates at Caxiuanã increased markedly following 3–4 yr of sustained drought, and at the Tapajós site, large increases in mortality were observed in the third year of throughfall exclusion (Nepstad et al., 2007). This similarity in sensitivity to drought occurred despite large differences in soil depth and texture between both sites (the Tapajós plot is located on an exceptionally deep (c. 100 m) clay soil while the Caxiuanã site is located on a 10–15 m deep sandy oxisol). It also occurs despite the fact that throughfall was only excluded in the wet season in Tapajós (Nepstad et al., 2002) but in both wet and dry seasons in Caxiuanã, although this distinction is somewhat artificial as dry season rainfall events have a higher probability at the Caxiuanã site.

Second, the relative increase in mortality was greatest in the largest trees. We found that mortality of trees in the smallest size class (< 20 cm dbh) was 40% greater in the TFE plot than in the control plot over the exclusion period, whereas mortality of medium trees was 128% greater in the TFE plot than in the control plot; but for the largest trees (> 40 cm dbh) this value rose to 194% relative to the control plot. This finding is reasonably consistent with results from the Tapajós site, where mortality of large trees (> 30 cm dbh in that study), increased by 445% in 3 yr,

compared with an increase of 98% for trees between 10 and 30 cm dbh. This result also agrees with several other studies of short-term ENSO-type droughts from Amazonia and other tropical areas, which report that large trees are most vulnerable to drought-induced mortality (Phillips, 2010). Possible reasons for this might include the greater evaporative demand and transpirational requirements of canopy-dominant trees, higher leaf temperatures at the top of the canopy (Fisher et al., 2010) and the longer length (and hence higher resistance) of the xylem water transport pathway in taller trees, increasing the tension which must be applied to move water from the soil to the leaf. Thus, longer path length may increase the risk of embolism in the xylem tissue leading to hydraulic dysfunction (Zhang et al., 2009).

Third, the magnitude of the relative increases in stem mortality at Tapajós and Caxiuanã are very similar, although we note the need for caution when directly comparing the experiments, as our data demonstrate that mortality rates can vary widely across years (Fig. 4). At Tapajós, the annual mortality of trees > 10 cm dbh over 5 yr of imposed drought was 5.7% in the TFE plot compared with 2.4% in the control plot (a relative increase of 138%; Brando et al., 2008), while, for the same length of exclusion (2002–2006), the mortality of trees > 10 cm dbh in Caxiuanã was 2.2% in the TFE plot compared with 1.45% in the control plot (an increase of 52%) and 1.0 ± 0.1% for other Caxiuanã plots (a relative increase of 120%). Over the whole 7 yr exclusion period, annual mortality rate in the Caxiuanã TFE plot was 2.5% compared with 1.25% in the control plot. Overall, a strong general picture emerges from this study that the response to drought is surprisingly similar in terms of magnitude and timing across both forests, despite differences in

soil type and species composition, even though the Tapajós forest appears to have been slightly more affected by the drought treatment in terms of some metrics.

Differential response of tree genera

We found evidence that the mortality rates of some genera increased more than for other genera under the drought treatment. This finding is strengthened by comparison with the Tapajós TFE of the 10 most common genera in the Caxiuanã TFE that were present in any meaningful quantity ($n \geq 5$) at Tapajós, where there was agreement between experiments in the direction of the response in 70% of cases. For example, Nepstad *et al.* (2007) also documented much higher mortality of *Eschweilera* and *Inga* following 3 yr of drought treatment (*Eschweilera*, 13%, *Inga*, 20%) than in the control (*Eschweilera*: 3%, *Inga*: 6%) at Tapajós, but found no evidence of increased mortality in *Manilkara* resulting from the drought. Moreover, Nepstad *et al.* (2007) also reported little or no effect of drought on mortality rates of *Licania*, *Lecythis*, *Protium* and *Tetragastris*, as also observed in this study. However, Nepstad *et al.* (2007) additionally reported increases in mortality of *Pouteria* and *Swartzia* under drought which were not observed in this study. Apparent differences in the drought vulnerability of specific taxa between sites may be a result of differences in the dominant species representing each genus at both sites. In Tapajós, for the genus *Pouteria*, *P. macrophylla* and *P. reticulata* are the dominant species, while *P. decorticans* and *P. cladantha* predominate at Caxiuanã. Similarly, *Swartzia recurva* is the dominant *Swartzia* species in Tapajós while *Swartzia racemosa* is the dominant *Swartzia* in Caxiuanã.

The reasons why some taxa appear to be more vulnerable to drought than others are not known. Differences in drought vulnerability may be driven by differences in the ability of plants to delay the onset of drought stress (e.g. through differences in rooting characteristics) or in their ability to maintain function despite water loss (Kursar *et al.*, 2009). Wood density has been shown to be strongly correlated with cavitation resistance (Hacke *et al.*, 2001). Phillips *et al.* (2009) found evidence of a weak relationship between wood density and drought-induced mortality in a basin-wide analysis of the impacts of the 2005 Amazonian drought. However, we found no difference between the wood density of trees that died in the TFE plot and those that died in the control plot over the exclusion period. This may be the result of the relatively narrow range of wood densities observed in this study, compared with previous studies where large mortality of light-wooded pioneers was reported (Slik, 2004).

The mechanistic basis of drought-driven mortality is currently an active area of debate. McDowell *et al.* (2008) used the concept of isohydry (Tardieu & Simonneau, 1998) to argue that isohydric plants, under conditions of prolonged stomatal closure, would steadily deplete their carbohydrate reserves and die of carbon starvation. Recent work showing that elevated temperature hastened the mortality of drought-stressed *Pinus edulis* by increasing respiration rates is consistent with the carbon starvation theory (Adams *et al.*, 2009). Other authors, however, have pointed out that direct evidence (i.e. observed depletion of carbon stores) for the carbon starvation theory is inconsistent with observations of high carbohydrate storage in trees approaching tree lines and during drought events (Leuzinger *et al.*, 2009; Sala, 2009; Sala & Hoch, 2009). Anisohydric plants, on the other hand, are considered to maintain higher stomatal conductance under drought conditions but face a greater risk of xylem embolism and potentially lower transpiration rates caused by a trade-off between xylem safety and efficiency (Hacke *et al.*, 2006). Leaf water potential measurements made in Caxiuanã suggest that trees at the site are generally isohydric (Fisher *et al.*, 2006) but the carbon starvation theory has yet to be tested in Amazonian TFEs.

Wider implications

The close agreement between the results of this study and those reported at the Tapajós TFE suggests that eastern Amazonian forests exhibit surprising uniformity in their response to multi-annual drought stress. These data are very important for earth system modelling purposes, as constraints on the range of sensitivity of Amazonian rainforest to prolonged drought stress have been generally lacking. The general picture is one in which an initial period of resilience (1–3 yr) is followed by large increases in tree mortality (*c.* 3–4 yr), especially amongst the larger, canopy-dominant trees (cf. Nepstad *et al.*, 2007; Meir *et al.*, 2009). The death of these large trees results in much lower standing biomass, instantaneous impacts on canopy function and considerable committed emissions of CO_2 to the atmosphere through future decomposition. The impact of such sustained drought events might possibly be even greater than demonstrated in this study, once the interaction between drought and fire is considered (Nepstad *et al.*, 2007; Meir *et al.*, 2008). The loss of large trees, which cast considerable shade on the forest understorey, allows more radiation to reach the forest floor, resulting in a drier, combustible litter layer (Ray *et al.*, 2005). The occurrence of fire greatly accelerates tree mortality (Cochrane *et al.*, 1999), and elevated temperatures may further compound drought and fire-driven carbon losses (Adams *et al.*, 2009; Galbraith *et al.*, 2010).

This study is also consistent with the basin-wide analysis of the impacts of the 2005 drought undertaken by Phillips *et al.* (2009), who found that most of the biomass loss was driven by accelerated tree mortality. It also agrees with a pan-tropical assessment of drought-driven mortality in which large trees were found to be the most vulnerable to tropical forest droughts (Phillips, 2010). These data all

point towards a generality in the response of rainforests to drought, at least in the mode of the response (death of large overstorey trees), although differences may exist regionally in the drought thresholds associated with the onset of mortality, which will likely depend on such factors as the shallowness of the soils and the effects of differences in species composition.

A further and intriguing consequence of a longer-term change to a drier climate may be the differential loss of some species and genera. Species with weak performance during drought, or a poor ability to colonize space during drought, may be excluded from progressively drier conditions (Engelbrecht *et al.*, 2007), resulting in forest ecosystems with lower biodiversity (Butt *et al.*, 2008) and very different functional properties (Fisher *et al.*, 2010). Results from the kind of long-term manipulation study reported here are proving increasingly useful for understanding these complex climate–forest interactions, especially as the experimental treatment period is extended (Hobbie *et al.*, 2003).

Acknowledgements

References

Abrams MD. 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiology* 7: 227–238.

Adams HD, Guardiola-Claramonte M, Barron-Gafford GA, Villegas JC, Breshears DD, Zou CB, Troch PA, Huxman TE. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences, USA* 106: 7063–7066.

Aiba SI, Kitayama K. 2002. Effects of the 1997–98 El Nino drought on rain forests of mount Kinabalu, Borneo. *Journal of Tropical Ecology* 18: 215–230.

Alencar A, Nepstad D, Diaz MDV. 2006. Forest understory fire in the Brazilian Amazon in ENSO and non-ENSO years: area burned and committed carbon emissions. *Earth Interactions* 10: 1–17. Paper 6.

Aragão L, Malhi Y, Barbier N, Lima A, Shimabukuro Y, Anderson L, Saatchi S. 2008. Interactions between rainfall, deforestation and fires during recent years in the Brazilian Amazonia. *Philosophical Transactions of the Royal Society B-Biological Sciences* 363: 1779–1785.

Araújo TM, Higuchi N, Carvalho JA. 1999. Comparison of formulae for biomass content determination in a tropical forest site in the state of Pará, Brazil. *Forest Ecology and Management* 117: 43–52.

Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen TJ, Laurance SG, Laurance WF *et al.* 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology* 10: 545–562.

Betts RA, Cox PM, Collins M, Harris PP, Huntingford C, Jones CD. 2004. The role of ecosystem-atmosphere interactions in simulated Amazonian precipitation decrease and forest dieback under global climate warming. *Theoretical and Applied Climatology* 78: 157–175.

Brando PM, Nepstad DC, Davidson EA, Trumbore SE, 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.

Brown S. 1997. *Estimating biomass and biomass change of tropical forests: a primer*. Rome, Italy: United Nations Food and Agriculture Organization, FAO Forestry Paper 134.

Butt N, Malhi Y, Phillips OL, New M. 2008. Floristic and functional affiliations of woody plants with climate in western Amazonia. *Journal of Biogeography* 35: 939–950.

Carswell FE, da Costa ACL, Palheta M, Malhi Y, Meir P, de Costa J, Ruivo K, Leal SM, Costa JMN, Clement RJ *et al.* 2002. Seasonality in CO_2 and H_2O flux at an eastern Amazonian rain forest. *Journal of Geophysical Research* 107: 8076.

Carvalho JA, Higuchi N, Araújo TM, Santos JC. 1998. Combustion completeness in a rainforest clearing experiment in Manaus, Brazil. *Journal of Geophysical Research* 103: 13199–13915.

Chambers JQ, dos Santos J, Ribeiro RJ, Higuchi N. 2001. Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *Forest Ecology and Management* 152: 73–84.

Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster H, Fromard F, Higuchi N, Kira T *et al.* 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87–99.

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

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

Condit R. 1998. *Tropical Forest Census Plots*. Springer-Verlag, Berlin, and R. G. Landes Company: Georgetown, Texas.

Condit R, Hubbell SP, Foster RB. 1995. Mortality-rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65: 419–439.

Costa MH, Foley JA. 2000. Combined effects of deforestation and doubled atmospheric CO_2 concentrations on the climate of Amazonia. *Journal of Climate* 13: 18–34.

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408: 184–187.

Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447: 80–82.

Fearnside PM. 1997. Wood density for estimating forest biomass in Brazilian Amazonia. *Forest Ecology and Management* 90: 59–87.

Fisher RA, McDowell N, Purves D, Moorcroft P, Sitch S, Cox P, Huntingford C, Meir P, Woodward FI. 2010. Assessing uncertainties in a second-generation dynamic vegetation model due to ecological scale limitations. *New Phytologist*, doi: 10.1111/j.1469-8137.2010.03340.x.

Fisher RA, Williams M, Da Costa AL, Malhi Y, Da Costa RF, Almeida S, 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.

Fisher RA, Williams M, Do Vale RL, Da Costa AL, Meir P. 2006. Evidence from Amazonian forests is consistent with isohydric control of leaf water potential. *Plant, Cell & Environment* 29: 151–165.

Fonty E, Sarthou C, Larpin D, Ponge J. 2009. A 10-year decrease in plant species richness on a neotropical inselberg: detrimental effects of global warming? *Global Change Biology* 15: 2360–2374.

Galbraith D, Levy P, Sitch S, Huntingford C, Cox P, Williams M, Meir P. 2010. Multiple mechanisms of Amazonian forest biomass losses in three Dynamic Global Vegetation Models (DGVMs) under climate change. *New Phytologist*, doi: 10.1111/j.1469-8137.2010.03350.x.

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloch KA. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457–461.

Hacke UG, Sperry JS, Wheeler JK, Castro L. 2006. Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiology* 26: 689–701.

Higuchi N, Santos J, Ribeiro RJ, Minette L, Biot Y. 1998. Biomassa da parte aérea da vegetação da Floresta Tropical Úmida de Terra-Firme da Amazônia Brasileira. *Acta Amazônica* 28: 153–166.

Hobbie JE, Carpenter SR, Grimm NB, Gosz JR, Seastedt TR. 2003. The US long term ecological research program. *BioScience* 53: 21–32.

Hoffmann WA, Schroeder W, Jackson RB. 2003. Regional feedbacks among fire, climate, and tropical deforestation. *Journal of Geophysical Research-Atmospheres* 108 (D23): 4721.

Hopkins MJG. 2007. Modelling the known and unknown plant biodiversity of the Amazon basin. *Journal of Biogeography* 34: 1400–1411.

Houghton RA, Lawrence KT, Hackler JL, Brown S. 2001. The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. *Global Change Biology* 7: 731–746.

Hurlbert SH. 2004. On misinterpretations of pseudoreplication and related matters: a reply to Oksanen. *Oikos* 104: 591–597.

Keller M, Palace M, Hurtt G. 2001. Biomass estimation in the Tapajós national forest, Brazil – examination of sampling and allometric uncertainties. *Forest Ecology and Management* 154: 371–382.

Kursar TA, Engelbrecht BMJ, Burke A, Tyree MT, El Omari B, Giraldo JP. 2009. Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Functional Ecology* 23: 93–102.

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

Leighton M, Wirawan N. 1984. Catastrophic drought and fire in Borneo tropical rain forest associated with 1982–1983 El Nino southern oscillation event. In: Prance GT, ed. *Tropical rain forest and world atmosphere*. New York, NY, USA: AAAS, 75–102.

Leuzinger S, Bigler C, Wolf A, Korner C. 2009. Poor methodology for predicting large-scale tree die-off. *Proceedings of the National Academy of Sciences, USA* 106: E106.

Lewis SL, Phillips OL, Sheil D, Vinceti B, Baker TR, Brown S, Graham AW, Higuchi N, Hilbert DW, Laurance WF, Lejoly J, et al. 2004. Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. *Journal of Ecology* 92: 929–944.

Li WH, Fu R, Dickinson RE. 2006. Rainfall and its seasonality over the Amazon in the 21st century as assessed by the coupled models for the IPCC AR4. *Journal of Geophysical Research-Atmospheres* 111: D02111.

Likens GE, Bormann FH, Johnson NM, Fisher DW, Pierce RS. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecological Monographs* 40: 23–47.

Lisboa PLB, Ferraz MG. 1999. *Estação Científica Ferreira Penna*. Belém, Brazil: CNPq/Museu Paraense Emílio Goeldi, 151.

Malhi Y, Aragão LEOC, Galbraith D, Huntingford C, Fisher R, Zelazowski P, Sitch S, McSweeney C, Meir P. 2009a. Exploring the likelihood and mechanism of a climate-change induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences, USA* 49: 20610–20615.

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

Malhi Y, Wood D, Baker TR, Wright J, Phillips OL, Cochrane T, Meir P, Chave J, Almeida S, Arroyo L et al. 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology* 12: 1107–1138.

van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fule PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH et al. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323: 521–524.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG et al. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178: 719–739.

Meir P, Brando PM, Nepstad D, Vasconcelos S, Costa ACL, Davidson E, Almeida S, Fisher RA, Sotta ED, Zarin D, et al. 2009. The effects of drought on Amazonian rain forests. In: Gash J, Keller M, Bustamante M, Silva Dias P, eds. *Amazonia and Global Change. Geophysics Monograph Series*. Washington, DC, USA: AGU, vol. 186, pp 429–449.

Meir P, Metcalfe DB, Costa ACL, Fisher RA. 2008. The fate of assimilated carbon during drought: impacts on respiration in Amazon rainforests. *Philosophical Transactions of the Royal Society B-Biological Sciences* 363: 1849–1855.

Metcalfe D, Phillips OL, Baker T, Brienen R, Chao KJ, Silva J. 2009. *Measuring tropical forest carbon allocation and cycling: RAINFOR field manual.* http://www.geog.leeds.ac.uk/projects/rainfor/pages/manuals_eng.html

Nakagawa M, Tanaka K, Nakashizuka T, Ohkubo T, Kato T, Maeda T, Sato K, Miguchi H, Nagamasu H, Ogino K. 2000. Impact of severe drought associated with the 1997–1998 El Nino in a tropical forest in Sarawak. *Journal of Tropical Ecology* 16: 355–367.

Nepstad DC, Moutinho P, Dias-Filho MB, Davidson E, Cardinot G, Markewitz D, Figueiredo R, Vianna N, Chambers J, Ray D, Guerreiros JB, et al. 2002. The effects of partial throughfall exclusion on canopy processes, aboveground production and biogeochemistry of an Amazon forest. *Journal of Geophysical Research* 107: D20.

Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G. 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology* 88: 2259–2269.

Nogueira EM, Fearnside PM, Nelson BW, Barbosa RI, Keizer EWH. 2008. Estimates of forest biomass in the Brazilian Amazon: new allometric equations and adjustments to biomass from wood-volume inventories. *Forest Ecology and Management* 256: 1853–1867.

Ostle NJ, Smith P, Fisher R, Woodward FI, Fisher JB, Smith JU, Galbraith D, Levy P, Meir P, McNamara NP et al. 2009. Integrating plant-soil interactions into global carbon cycle models. *Journal of Ecology* 97: 851–863.

Phillips OL, Aragão L, Lewis SL, Fisher JB, Lloyd J, Lopez-González G, Malhi Y, Monteagudo A, Peacock J, Quesada CA et al. 2009. Drought sensitivity of the Amazon rainforest. *Science* 323: 1344–1347.

Phillips OL, van der Heijden G, Lewis SL, Lopez-Gonzalez G, Aragao LEOC, Lloyd JJ, Malhi Y, Monteagudo A, Almeida S, Davila EA, et al. 2010. Drought-mortality relationships for tropical forests. *New Phytologist*, doi: 10.1111/j.1469-8137.2010.03359.x

Ray D, Nepstad D, Moutinho P. 2005. Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. *Ecological Applications* 15: 1664–1678.

Rolim SG, Jesus RM, Nascimento HEM, do Couto HTZ, Chambers JQ. 2005. Biomass change in an atlantic tropical moist forest: the ENSO

effect in permanent sample plots over a 22-year period. *Oecologia* **142**: 238–246.

Ruivo M, Cunha E. 2003. Mineral and organic components in archaeological black earth and yellow latosol in Caxiuanã, Amazon, Brazil. In: Tiezzi E, Brebbia CA, Uso JL, eds. *Ecosystems and sustainable development*. Southampton, UK: WIT Press, 1113–1121.

Saatchi SS, Houghton RA, Alvala RCDS, Soares JV, Yu Y. 2007. Distribution of aboveground live biomass in the Amazon Basin. *Global Change Biology* **13**: 816–837.

Sala A. 2009. Lack of direct evidence for the carbon-starvation hypothesis to explain drought-induced mortality in trees. *Proceedings of the National Academy of Sciences, USA* **106**: E68.

Sala A, Hoch G. 2009. Height-related growth declines in ponderosa pine are not due to carbon limitation. *Plant, Cell & Environment* **32**: 22–30.

Sheil D, May RM. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* **84**: 91–100.

Slik JWF. 2004. El Nino droughts and their effects on tree species composition and diversity in tropical rain forests. *Oecologia* **141**: 114–120.

Sombroek W. 2001. Spatial and temporal patterns of Amazon rainfall – consequences for the planning of agricultural occupation and the protection of primary forests. *Ambio* **30**: 388–396.

ter Steege H, Pitman N, Sabatier D, Castellanos H, van der Hout P, Daly SC, Silveira M, Phillips OL, Vasquéz R, van Andel T *et al.* 2003. A spatial model of tree alpha-diversity and tree density for the Amazon. *Biodiversity and Conservation* **12**: 2255–2277.

Tardieu F, Simonneau T. 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *Journal of Experimental Botany* **49**: 419–432.

Van Nieuwstadt MGL, Sheil D. 2005. Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *Journal of Ecology* **93**: 191–201.

Williams M, Rastetter EB, Fernandes DN, Goulden ML, Wofsy SC, Shaver GR, Melillo JM, Munger JW, Fan SM, Nadelhoffer KJ. 1996. Modelling the soil-plant-atmosphere continuum in a Quercus-Acer stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant, Cell & Environment* **19**: 911–927.

Williamson GB, Laurance WF, Oliveira AA, Delamonica P, Gascon C, Lovejoy TE, Pohl L. 2000. Amazonian tree mortality during the 1997 El Nino drought. *Conservation Biology* **14**: 1538–1542.

Zanne AE, Lopez-González G, Coomes DA, Ilic J, Jansen S, Lewis SL, Miller RB, Swenson NG, Wiemann MC, Chave J. 2009. *Global wood density database*. Dryad. Identifier: http://hdl.handle.net/10255/dryad.235

Zhang YJ, Meinzer FC, Hao GY, Scholz FG, Bucci SJ, Takahashi FSC, Villalobos-Vega R, Giraldo JP, Cao KF, Hoffmann WA *et al.* 2009. Size-dependent mortality in a neotropical savanna tree: the role of height-related adjustments in hydraulic architecture and carbon allocation. *Plant, Cell & Environment* **32**: 1456–1466.