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Threshold Responses to Soil Moisture Deficit by Trees and Soil in Tropical Rain Forests: Insights from Field Experiments

PATRICK MEIR, TANA E. WOOD, DAVID R. GALBRAITH, PAULO M. BRANDO, ANTONIO C. L. DA COSTA, LUCY ROWLAND, AND LEANDRO V. FERREIRA

Many tropical rain forest regions are at risk of increased future drought. The net effects of drought on forest ecosystem functioning will be substantial if important ecological thresholds are passed. However, understanding and predicting these effects is challenging using observational studies alone. Field-based rainfall exclusion (canopy throughfall exclusion; TFE) experiments can offer mechanistic insight into the response to extended or severe drought and can be used to help improve model-based simulations, which are currently inadequate. Only eight TFE experiments have been reported for tropical rain forests. We examine them, synthesizing key results and focusing on two processes that have shown threshold behavior in response to drought: (1) tree mortality and (2) the efflux of carbon dioxide from soil, soil respiration. We show that: (a) where tested using large-scale field experiments, tropical rain forest tree mortality is resistant to long-term soil moisture deficit up to a threshold of 50% of the water that is extractable by vegetation from the soil, but high mortality occurs beyond this value, with evidence from one site of increased autotrophic respiration, and (b) soil respiration reaches its peak value in response to soil moisture at significantly higher soil moisture content for clay-rich soils than for clay-poor soils. This first synthesis of tropical TFE experiments offers the hypothesis that low soil moisture–related thresholds for key stress responses in soil and vegetation may prove to be widely applicable across tropical rain forests despite the diversity of these forests.

Keywords: drought, tropical rain forest, tree mortality, physiology, soil respiration

In the last two decades, examples of extremes in rainfall have been observed pantropically, including exceptional El Niño Southern Oscillation events, two once-in-a-century drought events across Amazonia in 2005 and 2010, and recent extended declines in dry season rainfall (Marengo et al. 2011, Fu et al. 2013). Two important processes in forested ecosystems that may change substantially in response to altered moisture conditions, even in the absence of fire, are tree mortality and the emission of carbon dioxide (CO2) from soil, usually referred to as soil respiration (Davidson et al. 2006, Allen et al. 2010). Changes in both have the capacity to cause globally significant alterations to ecosystem functioning and atmospheric CO2 concentration this century. However, the understanding needed to constrain tropical forest responses to projected changes in rainfall remains limited (Meir and Woodward 2010).

Observational studies have provided insights into the response by tropical rain forests to reductions in soil moisture...
availability. Early flux measurements demonstrated varying degrees of daily and seasonal sensitivity to soil moisture in the carbon cycle of tropical rain forest (Grace et al. 1995, Malhi et al. 1998, Araujo et al. 2002, Saleska et al. 2003, Kumagai and Kume 2012). Plot-based observations of tree growth, recruitment and mortality have also identified high sensitivity to short-term severe drought in all major tropical regions (Meir and Grace 2005, Phillips et al. 2010). However, a lack of detailed component-scale flux data has limited process-level interpretation, especially below ground (Meir et al. 2008). Forward modeling of vegetation and soil processes for tropical forests against future climate scenarios remains in its infancy, and recent analyses using dynamic global vegetation models (used, e.g., in Earth system models) have highlighted both model insensitivity to moisture deficit in some processes such as tree mortality, and model oversensitivity to temperature in others such as respiration (Galbraith et al. 2010, Powell et al. 2013). There also remain gaps in understanding of plant physiological responses to drought, associated processes such as insect or pathogen attack, and the differing effects of the extremity and the duration of the climatic drivers (Anderegg et al. 2013, McDowell et al. 2013). Globally, there is a paucity of relevant data to inform vegetation models on these questions, and although the effects of forest loss from drought could be large (Reichstein et al. 2013), nowhere is this data gap more obvious than in the tropics, especially with respect to the few rainfall manipulation experiments that have been implemented to date in tropical rain forests. We examine those experiments here.

Experimental reduction of soil moisture is achieved in forests by deflecting the rainfall that penetrates a canopy (throughfall) away from treatment plots using a drainage structure installed 1–2 meters (m) above the forest floor (figure 1). This throughfall exclusion (TFE) approach complements studies of natural drought because soil moisture can be altered beyond normal ranges, independently of other climate drivers, and at large or small scales. This is valuable in circumstances in which ecological treatment responses may become non-linear or alter qualitatively over different time scales (Leuzinger et al. 2011, Wu et al. 2011). Eight TFE studies have been implemented in tropical rain forests in recent years (table 1). They vary in plot size, treatment duration and measurements, and this limits comprehensive detailed comparison, so here we consider the responses of two widely measured processes that have shown threshold behavior in response to low soil moisture availability and have the potential to significantly alter ecosystem functioning: tree mortality and soil respiration. We combine data sets from different studies (box 1) to test the broad hypotheses that: (a) the increase in tropical rain forest tree mortality during extended soil moisture deficit is non-linear with respect to soil moisture deficit, and this response function is similar across sites, and (b) soil texture explains

Figure 1. Large- and small-scale throughfall exclusion (TFE) structures in tropical rain forest, placed 0.5–2 meters aboveground level. (a) Caxiuanã National Forest, Pará, Brazil (treatment size: 1 hectare). (b) Luquillo Experimental Forest, Puerto Rico (treatment size: 1.5 square meters).
the observed differences in the responses by soil respiration to reduced soil moisture. We also consider how the TFE approach is useful for developing ecological insight into ecosystem–environment responses over multiple timescales.

**Vegetation responses to ecosystem-scale rainfall exclusion**

The sudden reduction in live biomass resulting from widespread drought-induced tree mortality has received much attention in the last 5–10 years (Breshears et al. 2005, Allen et al. 2010, McDowell et al. 2011). There is evidence that drought and warming events have already led to notable forest dieback events globally, with the evidence that drought and warming events have already occurred in the late 20th century (Allen et al. 2010, McDowell et al. 2011, O'Brian et al. 2014). Current analysis, mainly from temperate-zone forests, supports all three explanations of varying degrees and this lack of clarity hampers attempts to model mortality mechanistically (Sala et al. 2012).

A pantropical analysis of the effects of natural drought on tree mortality (Phillips et al. 2010) used a synthesis of forest plot data (typically 1 hectare [ha]) focused primarily on Amazonia during the 2005 drought in that region, and on Southeast Asia during the 1997–1998 El Niño to suggest a relationship between soil moisture deficit and increased mortality, with both linear and nonlinear relationships between soil moisture deficit and tree mortality considered. Averaged mortality data from two large-scale TFE experiments in Amazonian rain forest were apparently consistent with observations from natural drought at regional scale (Phillips et al. 2010), but the rich longitudinal data and ecosystem process modeling outcomes from these experiments (Fisher et al. 2007, Nepstad et al. 2007, Brando et al. 2008, da Costa et al. 2010) were not explored. More recently, a third large-scale TFE experiment has been reported for Southeast Asia, providing additional insight into the effects of drought in an aseasonal rain forest (Schuldt et al. 2011, Moser et al. 2014). These three soil moisture manipulation experiments are the only such ecosystem-scale experiments reported for tropical rain forest and therefore offer unique insight into the drought–mortality relationship for one of the world’s key biomes. Focussing on tree mortality, we compare the results and combine data from these studies to address hypothesis (a).

Each of the three ecosystem-scale TFE experiment sites support species-rich, old-growth rain forest, but each differs in annual rainfall and soil characteristics (table 1). The two Amazonian experiments (Meir et al. 2009), in the Brazilian state of Pará in the east of the region, are the ‘Escaflor’ experiment at Caxiuanã National Forest (CAX); and the ‘Seca Floresta’ experiment at Tapajós National Forest (TAP). Annual precipitation at CAX and TAP is similar at 2000–2300 millimeters (mm), and both experience a significant dry season, with stronger seasonality at TAP, whereas the Sulawesi Throughfall Exclusion Experiment

<table>
<thead>
<tr>
<th>Site ID</th>
<th>Elevation (in meters)</th>
<th>MAP</th>
<th>MAT</th>
<th>Soil type</th>
<th>Soil depth (in meters)</th>
<th>Aboveground biomass (in megagrams of carbon per hectare)</th>
<th>Percentage rain excluded</th>
<th>TFE length (in months)</th>
<th>Plot size (in square meters)</th>
<th>Rs</th>
</tr>
</thead>
<tbody>
<tr>
<td>CAXa</td>
<td>15</td>
<td>2300</td>
<td>26</td>
<td>Oxisol</td>
<td>10–15</td>
<td>215</td>
<td>50</td>
<td>120</td>
<td>10 000</td>
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<tr>
<td>TAPb</td>
<td>150</td>
<td>2000</td>
<td>27</td>
<td>Oxisol</td>
<td>&gt;80</td>
<td>270</td>
<td>50</td>
<td>72</td>
<td>10 000</td>
<td>2.6</td>
</tr>
<tr>
<td>SULc</td>
<td>1050</td>
<td>2900</td>
<td>21</td>
<td>Nitisol</td>
<td>&gt;4</td>
<td>300</td>
<td>50–80</td>
<td>24</td>
<td>1600</td>
<td>3.2</td>
</tr>
<tr>
<td>FAZd</td>
<td>100d</td>
<td>1800</td>
<td>26</td>
<td>Oxisol</td>
<td>&gt;18</td>
<td>260</td>
<td>50</td>
<td>12</td>
<td>100</td>
<td>2.7</td>
</tr>
<tr>
<td>OSAe</td>
<td>50</td>
<td>5000</td>
<td>27</td>
<td>Ultisol</td>
<td>n/a</td>
<td>180</td>
<td>50</td>
<td>12</td>
<td>5.76</td>
<td>3.0</td>
</tr>
<tr>
<td>LEFslopef</td>
<td>350</td>
<td>3500</td>
<td>23</td>
<td>Ultisol</td>
<td>33 m</td>
<td>312</td>
<td>100</td>
<td>3</td>
<td>1.54</td>
<td>3.6</td>
</tr>
<tr>
<td>LEFvalleyf</td>
<td>350</td>
<td>3500</td>
<td>23</td>
<td>Ultisol</td>
<td>20 m</td>
<td>186</td>
<td>100</td>
<td>3</td>
<td>1.54</td>
<td>3.4</td>
</tr>
</tbody>
</table>

Note: Detailed locations are in the reference citations. Elevation is in meters (m) above sea level. Abbreviations: CAX, Caxiuanã National Forest Reserve, Pará, Brazil; FAZ, Fazenda Vitoria, Pará, Brazil; LEF, Luquillo Experimental Forest, Puerto Rico; MAP, mean annual precipitation (in millimeters); MAT, the mean annual temperature (degrees Celsius); OSA, Osa Peninsula, Costa Rica; Rs, mean annual soil carbon dioxide efflux from undisturbed forest (in micromols CO₂ per square meter per second); SUL, Pono Valley, Lore Lindu National Park, Central Sulawesi, Indonesia; TAP, Tapajós National Forest Reserve, Pará, Brazil. aMeir et al. 2009. bBrando et al. 2008. cSchuldt et al. 2011, Moser et al. 2014. dCattanio et al. 2002. eCleveland et al. 2010. fWood and Silver 2012, Scatena and Lugo 1995. gEstimated.
Box 1. Analysis of combined data sets from multiple studies.

Large-scale TFE is required to examine experimentally how soil moisture deficit affects ecosystem-level metrics of ecosystem function such as tree mortality. At all three such tropical rain forest experiments, CAX, TAP, and SUL, there was no significant change in tree mortality for the first 2 years of TFE, but whilst the experiment at SUL was terminated after 2 years, mortality increased substantially at CAX and TAP from year 3 onward (figure 2a; da Costa et al. 2010, Moser et al. 2014). Tree mortality and soil moisture data at CAX and TAP were combined and analysed to examine hypothesis (a). Soil moisture availability was expressed as relative extractable water (REW) over the top 3 m of soil. REW is defined as the fraction of the maximum extractable water content (plant available water, \( \text{PAW}_{\text{max}} \)) for each soil layer. \( \text{PAW}_{\text{max}} \) refers to the soil moisture available between field capacity (\( \theta_{\text{fc}} \)) typically taken to be ~33 kilopascals (kPa) and wilting point (\( \theta_{\text{w}} \)), typically taken to be ~1500 kPa. However, it is very difficult to obtain accurate values of \( \theta_{\text{fc}} \) and \( \theta_{\text{w}} \). These can be derived from soil water characteristic curves where available, or from the use of pedotransfer functions, but such functions are highly uncertain and the actual wilting point (soil water potential at which water uptake ceases) is rarely known. Here, we use a very simple metric to calculate REW, in which we set \( \theta_{\text{fc}} \) to be equal to the minimum volumetric water content (VWC) value observed (\( \theta_{\text{min}} \)) and \( \theta_{\text{w}} \) to be equal to the observed maximum monthly mean VWC. Such a simple approach is consistent with previous studies (Granier et al. 2000, Nepstad et al. 2007) and provides us with a comparable metric with which to estimate plant water availability across plots. Therefore, for each soil layer \( i \), REW is estimated as

\[
\text{REW}_i = \frac{\theta - \theta_{\text{min}}}{\theta_{\text{max}} - \theta_{\text{min}}}
\]

in which \( \theta \) is the actual volumetric water content, \( \theta_{\text{min}} \) is the minimum volumetric water content and \( \theta_{\text{max}} \) is the maximum monthly mean VWC. We use detailed soil profile VWC measurements and validated model results (Fisher et al. 2006, 2007, Nepstad et al. 2007), weighting layer-specific REW values by soil layer depths to calculate REW for the top 3 m. We computed annual values of REW for each year in the control and treatment plots and related these to annual values of stem and biomass mortality. The relationship between REW and mortality was examined using linear and nonlinear fits, including piecewise regression, using the statistical package R (R 2.14.2, R-project software, www.r-project.org, R 2.14.2). The vulnerability to mortality of the most well-represented taxonomic groups at each site was also examined by comparing mortality between treatment and control plots (da Costa et al. 2010).

Soil processes in tropical forests have been studied using TFE treatments varying in size from 1.5 m\(^2\) to 1 ha, and in duration from seasonal TFE to a decade-long experiment (table 1). For the soil respiration (\( R_s \)) analysis (hypothesis (b)), site level data were collated from each: mean annual precipitation (MAP), mean annual temperature (MAT), volumetric soil moisture content (percent), soil texture (percent clay, silt, and sand), available nutrient pools (total phosphorus, total nitrogen, available phosphorous, nitrate and ammonium) together with mean surface emissions of CO\(_2\) (\( R_s \)). As most TFE treatments were short in duration (3 months–2 years), analysis of combined data sets was focused on the short-term phase of soil moisture reduction. General linear regression was used to examine single and multivariate relationships among soil moisture content, soil texture and soil gas emission metrics during soil moisture deficit. The threshold soil moisture content at which maximum \( R_s \) was observed was analysed using a dataset expanded to incorporate a wider range of soil texture values by also including observational studies from tropical rainforest (listed in appendix S1).

The responses to TFE can be distinguished by timescale into short-term (0–2 years) and medium-term (3–7 years) effects, although longer-term phases of biomass loss and recovery can also be expected, consistent with basic ecological principles (Shugart 1997, da Costa et al. 2014). The transition from short timescales in the TFE data was characterised by the emergence of substantial changes in tree mortality rates (figures 2 and 3), and at least at one site (CAX), in autotrophic physiology. A summary of responses is provided in box 2, with the mortality data examined below.

Similarity in vegetation responses to extended soil moisture deficit? A surprising degree of similarity in response to the TFE treatments was observed at all three experiments, despite their differing locations, soils, species assemblages and climate. Aboveground wood production (for stems with dbh more than 10 centimeters) declined by 30%–40% (da Costa et al. 2010, Moser et al. 2014) but at no site did tree mortality decline by more than 30%.
change for the first 2 years of TFE, suggesting widespread initial resistance in the vegetation to soil moisture deficit (figure 2a). Response data over more than 2 years of TFE are only available from TAP and CAX, but despite the large differences in soil profiles at each site, a consistent pattern emerged, with tree mortality rising rapidly after 2 years of TFE, committing 20%–25% of the original standing biomass (215–270 Mg C per ha) to the atmosphere through future decomposition (Brando et al. 2008, da Costa et al. 2010). Large trees (dbh more than 40 centimeters), which comprised 58%–62% of the original biomass, were the most vulnerable at both CAX and TAP (da Costa et al. 2010), as also observed following natural severe droughts (Phillips et al. 2010), and there was also some phylogenetic consistency among the experiments in terms of the most and least vulnerable taxa. At the family level, the Fagaceae were sensitive to TFE in both Sulawesi and Amazonia (da Costa et al. 2010, Moser et al. 2014). Within the Amazon at both CAX and TAP, the genus Eschweilera was very sensitive to the TFE treatment, whereas Licania was notably resistant (Nepstad et al. 2007, da Costa et al. 2010); among other taxa the mortality response varied up to fourfold (figure 2b). These data provide unique insight into the long-term composition of tropical rain forest following severe drought. They also offer a focus for efforts to quantify the consequences for ecosystem functioning of drought-related tree mortality, and to test for convergence among drought-tolerant species groups in plant functional traits (Oliveira et al. 2014) and resistance to biotic attack.

Although soil moisture content by volume is commonly measured in ecosystem process studies, it does not quantify the water available to plants because of site-based differences in soil physical properties and plant moisture acquisition strategies (Fisher et al. 2008). To account for this we used a measure of the water available to vegetation, the relative extractable water, REW (box 1). Elsewhere, water deficit metrics for tropical forest regions have been calculated from rainfall estimates and an assumed transpiration rate (e.g., Phillips et al. 2010, Gatti et al. 2014). The REW metric is calculated as a fraction of the maximum water shown to be extractable at each site; therefore, although less easily applicable at a large scale, it provides a more ecologically informative metric by taking account of differences among soils in water availability to plants.

Although the dry season is slightly stronger at TAP than at CAX, there was no marked difference between sites in the year-to-year variability in the minimum observed REW, of 0.2 (figure 3). The mortality responses to REW relative to background rates were very similar, despite large edaphic differences between the sites. Mortality showed no trend when soil moisture availability was high, at REW values greater than 0.5, although there was interannual variability of 100%–200% in background mortality rates (figure 3). However, as REW declined below 0.5, a significant fourfold linear increase in mortality up to 700% was observed, indicative of a new and similar response phase in both forest ecosystems. The mortality increase varied at both sites with

![Figure 2](http://bioscience.oxfordjournals.org)
The observed mortality response to severe natural drought in the tropics (Meir and Grace 2005, Phillips et al. 2010) has in general been more rapid than in the TFE experiments. This likely reflects the additional stress that occurs during natural drought from the combination of increased maximum vapor pressure deficit and leaf temperatures in addition to soil moisture deficit (although foliar water uptake might have contributed to the slower mortality response in the TFE experiments). Phillips and colleagues (2010) also showed that aseasonal Bornean rainforests appeared to have larger mortality responses to natural drought than their more seasonal Amazonian counterparts. It is not clear whether these regional differences reflect differences in drought severity, soil properties or less well drought-adapted vegetation phenotypes. However, we speculate that at any one site, short term severe natural drought and high temperatures may cause significant hydraulic failure in leaves or leaf mortality, leading to rapid death for vulnerable individuals and taxa. By contrast, the effects of extended soil moisture deficit are likely to be characterized by reduced hydraulic function or a reduction in the availability of carbon resources from photosynthesis, together exposing trees to progressively higher risk from pest or pathogen attack, in addition to the failure in physiological processes. The stand-scale data from CAX show some consistency with the ecophysiological components of this interpretation. Notwithstanding the possibility of species-based variation in hydraulic and carbon-use traits, very strong canopy-scale reductions in hydraulic performance were observed in the short term at CAX (less than 1 year of TFE; Fisher et al. 2006, Fisher et al. 2007), whereas Metcalfe and colleagues (2010b) argued that beyond three years of TFE, as mortality increased, the droughted forest was also expending approximately 7 tons of carbon per ha per year more than it was acquiring through gross primary production, consistent with the notion of a declining reserve of stored carbon.

The TFE experiments inform our understanding of the effects of soil moisture reduction alone on mortality, but they do not necessarily specify the mechanism of tree death (e.g., McDowell et al. 2013). In a recent test of five dynamic global vegetation models using the TAP and CAX data, none replicated well the loss of biomass in response to the long-term TFE, with variance in model predictive skill reflecting the need for better representation of both moisture deficit effects on plant function and phenology, and of biomass loss processes (Powell et al. 2013). Separately, where six vegetation models explicitly representing both hydraulic and carbohydrate flux processes were tested against a two-species TFE experiment in the semiarid southeast United States, both hydraulic and carbon-based processes were implicated in the mortality process (McDowell et al. 2013). A second, more demanding, test would be to model the combined effects of atmospheric and edaphic drivers of severe natural

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drought stress on tree mortality. Representing the dominant mode(s) of tree death during a drought therefore remains a challenge, especially when the responses to drought may affect mortality risk over several years (Anderegg et al. 2013), creating lags in the drought–mortality relationship and its effects on ecosystem-scale processing of carbon and water. A tractable and physiologically meaningful way of modeling the multiple pathways to mortality may be to define a stress threshold beyond which death becomes likely because of physiological failure or biotic attack. A focus on mechanistically driven estimates of physiological stress leading singly or in combination to a threshold value beyond which mortality increases for given species groups could provide an heuristic and effective way to guide research on drought–mortality responses. Such an approach should be flexible enough to allow for mortality to occur rapidly—as well as after repeated or extended drought events—and therefore remain consistent with evidence from TFE experiments and natural drought events (Phillips et al. 2010, Anderegg et al. 2013, Barbeta et al. 2013). A threshold concept based only on carbon storage has been used in dynamic global vegetation models (e.g., Powell et al. 2013), but a metric that integrates both hydraulic and carbon-related responses, and probably with its principal locus in the leaf, may ultimately prove more flexible with respect to different locations and climate change scenarios; and it may also facilitate detection of increased mortality risk at large scales, via the use of rapidly developing remote sensing techniques (Asner et al. 2011).

**Responses by soil respiration to reductions in soil moisture**

Soil respiration ($R_s$) comprises the largest source of CO$_2$ to the atmosphere in the terrestrial carbon cycle and substantial changes in $R_s$ can alter the sign of net ecosystem productivity (Davidson et al. 2006, Meir et al. 2008). At a

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**Box 2. Short- and long-term responses by the vegetation to experimental soil moisture deficit.**

**Short-term responses (0–2 years): changes in canopy structure, tree growth and ecophysiology**

The TFE experiment at SUL was imposed for 2 years, whereas at CAX and TAP, the TFE treatment regime continued for several years. There was notable consistency in the response to TFE among sites despite differences in measurement programs. The short-term (0- to 2-year) response by growth to soil moisture deficit was similar, with a reduction in aboveground wood production ranging from 30% to 40% among all three sites. At CAX and TAP, there was a reduction in leaf area index (LAI, m$^2$ leaf area per m$^2$ ground area) by more than 20% over the first 2 years of the experiment (Meir et al. 2009). At SUL, LAI did not decline, but leaf number per distal branch declined implying a reduction in leaf bud development (Schuldt et al. 2011). The short-term physiological responses in the vegetation were consistent with these reductions in productivity. Maximum leaf photosynthesis was lower at TAP and CAX under soil moisture deficit. At CAX this was shown to be controlled hydraulically; maximum carboxylation capacity did not change significantly but maximum stomatal conductance was down-regulated, with consequent declines observed in sap flux by up to 40% (Fisher et al. 2007, Meir et al. 2009). An increase in the hydraulic resistance of the soil-to-atmosphere water pathway was observed at both CAX and SUL. A combination of soil and plant hydraulics data and soil-to-atmosphere process modeling for CAX indicated that in addition to the stomatal control, the principal locus of increased hydraulic resistance in response to soil moisture deficit was below ground (Fisher et al. 2006, 2007, 2008). At SUL, increased hydraulic resistance was observed in distal twig xylem tissue, with larger trees showing greater reductions in xylem-specific conductivity under soil moisture deficit (Schuldt et al. 2011). At TAP, nocturnal hydraulic redistribution in the root zone was shown to improve soil moisture availability for some trees over the first 2 years, although this process rapidly declined in importance subsequently (Markewitz et al. 2010). At CAX, a multilayer soil and canopy physiology model was developed and parameterised to simulate the response to drought. The model was validated using independent sap flux and soil moisture measurements, and used to quantify responses over the first 2 years of the TFE treatment: stand-level transpiration was estimated to decline by 40%, and gross primary productivity declined by 13%–14% (Fisher et al. 2007).

**A long-term increase in autotrophic respiration**

Only limited longer-term ecophysiological data are available, with a focus on autotrophic respiration at CAX. Leaf dark respiration ($R_{\text{dark}}$) increased at CAX during the first 7 years of TFE (Metcalfe et al. 2010a), leading to an increase in canopy respiration despite the reduction in LAI. $R_{\text{dark}}$ has been observed more frequently to decline with photosynthesis, although increases in $R_{\text{dark}}$ during drought have been noted for other forests, including elsewhere in Amazonia (Metcalfe et al. 2010a). The evidence from measurements of CO$_2$ flux from woody tissue and soil at CAX was consistent with this, suggesting that the long-term soil moisture deficit had led to a long-term increase in autotrophic respiration, perhaps in reparatory response to drought stress (Metcalfe et al. 2010b). If photosynthesis in Amazon rain forests declines during drought, and ecosystem respiration does not, there is potential for net ecosystem production (NEP) to switch from a net carbon sink (NEP more than 0) to a source (NEP less than 0; Meir et al. 2008, Rowland et al. 2014). Metcalfe and colleagues (2010b) summed all NPP and respiration terms for control and droughted forest and calculated that total carbon use by the droughted forest likely exceeded GPP. The analysis indicated that the droughted forest had a reduced carbon use efficiency (CUE = NPP/GPP) with respect to control forest, and was potentially acting as a net carbon source (i.e., NEP less than 0), although uncertainty terms were relatively large. New physiological measurements are needed to test the persistence of this finding, quantifying long-term (decadal-scale) responses to the TFE treatment in the key underlying respiratory, hydraulic and photosynthetic parameters.
single site, the response to soil moisture by $R_s$ is usually—
but not always—peaked, with lower $R_s$ values at high and
low soil moisture content (Davidson et al. 2006). Very wet
soils impose diffusion limitations on the supply of oxygen
to respiring cells and the surface emissions of CO$_2$, whereas
at the dry end, cellular desiccation and a reduced supply of
soluble carbon act to constrain $R_s$ (Davidson et al. 2006).
The soil moisture value at which the threshold, or maxi-
mum, $R_s$ occurs can vary among sites (Wood et al. 2013)
and is usually somewhere near field capacity, when optimal
gas and substrate diffusion co-occur. As with representing
mortality responses to drought, finding ways to generalize
these observations in an appropriate and scaleable manner
is an important goal, both to advance understanding and to
inform predictive models of ecosystem function.

Experimental TFE in tropical forests where soil processes
have been studied has been implemented at five sites in addi-
tion to the three ‘ecosystem-scale’ TFE experiments consid-
ered above. The study plots have varied in size from 1.5 m$^2$
to 1 ha, and the TFE treatments have varied in duration from
three months to a decade-long experiment (table 1). The
sites are all in tropical rain forest, range in mean annual
precipitation from 1800 mm to 5000 mm and have soils that
vary in texture and depth. There has been a correspond-
ingly large range in responses by $R_s$ to the TFE treatment:
where soil moisture was successfully reduced, responses in
$R_s$ ranged from no effect to a 48% decline (Cattânio et al.
2010b, van Straaten et al. 2011, Wood and Silver 2012). Numerous
explanations for the range in responses by $R_s$ to TFE have been put forward and reflect the diversity of pro-
cesses contributing to $R_s$, as well as possible differences in
TFE implementation. The range of hypothesised biophysical
responses include: differential responses of root, litter, and
soil organic matter to soil moisture status (Sotta et al. 2007,
von Straaten et al. 2011); differences in soil nutrient avail-
ability (Wood and Silver 2012); differences in rooting depth
(Davidson et al. 2008); and changes in dissolved organic
carbon concentrations together with oxygen availability
(Cleveland et al. 2010). We hypothesized that the variability
in $R_s$-moisture responses among studies might be explained
more generally by differences in the microscale structure
and properties of soil, and the related fine-scale effects on
the availability of moisture to microbes and roots. Despite
recent advances in quantifying soil physical properties for
some tropical regions (e.g., Amazonia; Mathews et al. 2014)
there remains a general lack of the soil physics measure-
ments needed to parameterise hydraulics models for the
tropics (Fisher et al. 2008). However, soil texture informa-
tion is widely available and potentially provides a first-order
proxy for moisture availability to chemical and biological
processes in soil. It forms the focus for our analysis address-
ing hypothesis (b) (see box 1).

**Influence of soil texture on soil respiration.** We did not observe
any consistent effect of rainfall, temperature, soil moisture,
Three out of eight throughfall exclusion studies reported a soil moisture–resistance followed by instability may be typical of the initial response by an ecosystem to continuous environmental stress (Scheffer and Carpenter 2003), although we also note the importance of accounting for lagged effects on longer-term ecological dynamics and ecosystem process stability. The soil moisture metric REW offers a simple and ecologically robust way of comparing tropical forest functioning on different soils and under different precipitation regimes, but the relationship with mortality needs to be tested in less seasonal tropical rain forests, such as in Southeast Asia, where soil or vegetation properties may vary substantially, and ideally further afield, in drier climates as well. Collectively, the data from TAP, CAX and SUL are consistent with notions of both hydraulic and metabolic limitation of trees under severe drought, but as for many temperate zone studies, they do not distinguish which process dominates the path to increased tree mortality, or whether increased susceptibility to biotic attack is ultimately the most important effect. This question remains a future challenge. Our second hypothesis (b), that soil texture explains the wide variance in $R_s$ responses to soil moisture content, was not supported in our TFE synthesis analysis. However, soil clay content was correlated strongly with the threshold soil moisture content for maximum $R_s$, with clay-rich soils requiring higher water content to yield peak $R_s$ (figure 4). Given the wide availability of soil texture data, the modulation of peak $R_s$ in relation to clay content may have general application in constraining models of $R_s$, depending on constraining models of $R_s$, depending on model complexity.

Although TFE experiments do not replicate all the climate drivers of a natural drought, by changing only soil moisture status, these large-scale manipulations do enable explicit testing of the soil moisture response functions embedded within ecosystem models (McDowell et al. 2013) and may also reveal unexpected process-level responses (box 2; Meir et al. 2008, Metcalfe et al. 2010a). The size of the treatment effect in such global change experiments has been argued to be smaller and ‘more realistic’ when experiments are conducted over long timescales and when multiple environmental treatments are combined (Leuzinger et al. 2011, Wu et al. 2011, Barbeta et al. 2013). However, the tropical rain forest TFE studies here only partially support this reasoning. For example, although there was a long-term decline in $R_s$ after 4 years of TFE at CAX (Metcalfe et al. 2010b), the effects of low soil moisture on the mortality of large trees was initially small, then peaked and subsequently declined over 10 years (figures 2 and 3; da Costa et al. 2014). Although some of the TFE results show a degree of consistency with mortality data obtained from natural severe droughts (Phillips et al. 2010), the more rapid path to tree mortality for some tropical trees following natural droughts, where vapor pressure deficit and leaf temperature extremes are combined with soil moisture deficit, also show that multitreatment effects on an ecosystem can be larger, or occur faster, than single-factor effects. Therefore, the combination, severity, and duration of drought events will likely affect different processes such as mortality, autotrophic respiration, and $R_s$ in different ways. The key is to acknowledge this complexity and use a combination of experimental and observational data to generate strong new model-testing frameworks, focusing on ecological processes and their interactions over different timescales.

**Conclusions**

The risk of increased drought in the twenty-first century may be high in some tropical regions (Fu et al. 2013,
Reichstein et al. 2013), but the sensitivity of tropical rainforests to drought is substantially higher than in many current dynamic global vegetation models (Galbraith et al. 2010, Huntingford et al. 2013), even before interactions between drought and fire are considered (Brando et al. 2014). The effects of drought on the functioning of a forested ecosystem take place at multiple interacting scales. Understanding and representing this in a sufficiently parsimonious and mechanistic way to enable prediction is a significant challenge for ecological and Earth system science, and is important for the environmental governance decisions which they influence (Meir and Woodward 2010).

Collectively, the eight TFE experiments to date in tropical rain forest show that despite large intersite variation, there is generality in the sensitivity of tropical rain forest trees and soil to significant soil moisture deficit. There are identifiable soil moisture thresholds for tree mortality and $R_b$ beyond which phases of rapid change can be expected, although wider testing is desirable. Mortality data from TFE experiments and observational studies are strongly consistent in showing high sensitivity to severe drought, especially in larger trees, but there are differences as well. For example, some mortality occurs more rapidly following severe natural droughts, and observational studies do not consider the dynamics resulting from longer-term drought. Integrated model, observational and experimental analysis is needed to probe and represent better the process interdependency causing both short- and longer-term ecological dynamics. However, our experimental data sets still only extend a little beyond a decade and this limits model validation exercises. The long-term TFE experiment data suggest that following rapid mortality among drought-sensitive taxa, some recovery might be expected, with a new and identifiable emergent species assemblage (da Costa et al. 2014). But what happens at multidecadal timescales or longer? This question is pressing, and achieving robust answers will require a combination of approaches in concert with those discussed here, including more use of long-term and spatially extensive observational data (e.g., Fauset et al. 2012) and of paleoecological inference (e.g., Zuidema et al. 2013).

Supplemental material

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