



Tree Physiology 33, 903–912  
doi:10.1093/treephys/tpt064



## Tree Physiology review

# An imperative need for global change research in tropical forests

Xuhui Zhou<sup>1,4</sup>, Yuling Fu<sup>2</sup>, Lingyan Zhou<sup>1</sup>, Bo Li<sup>1</sup> and Yiqi Luo<sup>3</sup>

<sup>1</sup>Coastal Ecosystems Research Station of Yangtze River Estuary, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, The Institute of Biodiversity Science, Fudan University, 220 Handan Road, Shanghai 200433, China; <sup>2</sup>The Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration (SHUES), East China Normal University, Shanghai 2000241, China; <sup>3</sup>Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK 73019, USA; <sup>4</sup>Corresponding author (zxuhui14@fudan.edu.cn)

Received February 6, 2013; accepted July 26, 2013; handling Editor Jörg-Peter Schnitzler

Tropical forests play a crucial role in regulating regional and global climate dynamics, and model projections suggest that rapid climate change may result in forest dieback or savannization. However, these predictions are largely based on results from leaf-level studies. How tropical forests respond and feedback to climate change is largely unknown at the ecosystem level. Several complementary approaches have been used to evaluate the effects of climate change on tropical forests, but the results are conflicting, largely due to confounding effects of multiple factors. Although altered precipitation and nitrogen deposition experiments have been conducted in tropical forests, large-scale warming and elevated carbon dioxide (CO<sub>2</sub>) manipulations are completely lacking, leaving many hypotheses and model predictions untested. Ecosystem-scale experiments to manipulate temperature and CO<sub>2</sub> concentration individually or in combination are thus urgently needed to examine their main and interactive effects on tropical forests. Such experiments will provide indispensable data and help gain essential knowledge on biogeochemical, hydrological and biophysical responses and feedbacks of tropical forests to climate change. These datasets can also inform regional and global models for predicting future states of tropical forests and climate systems. The success of such large-scale experiments in natural tropical forests will require an international framework to coordinate collaboration so as to meet the challenges in cost, technological infrastructure and scientific endeavor.

**Keywords:** carbon, climate change, elevated CO<sub>2</sub>, energy, tropical forests, warming, water.

## Introduction

Despite their relatively small coverage of the Earth's land surface (<10%), tropical forests provide a wide range of important services to humankind, such as maintenance of biodiversity, carbon (C) sequestration and climate regulation, as well as economic and recreational values (Hassan et al. 2005). Tropical forests harbor the largest terrestrial reservoir of biodiversity from the gene to the habit level, with more than half of the world's plant and animal species (Dirzo and Raven 2003). This biome contains up to 55% of global terrestrial C stocks (Pan et al. 2011), exchanges more water and carbon dioxide (CO<sub>2</sub>) with the atmosphere than any other one (Foley et al. 2005),

and accounts for at least one-third of global terrestrial net primary production (NPP; Phillips et al. 1998, Cleveland et al. 2011). In addition, >800 million people depend on tropical forests for fuel, food and income (Hassan et al. 2005). Tropical forests thus play a pivotal role in the functioning of the planet's natural and human systems.

Rapid climate change has already been found to significantly affect ecosystem structure and functioning in tropical forests (Bawa and Markham 1995, Corlett 2011). Field observations have shown that the growth rates of tropical trees declined considerably with subtle increases in average temperature, indicating their high sensitivity to temperature (Clark et al. 2003,

Feeley et al. 2007). Meanwhile, considerable evidence has mounted that climate change, especially warming, has caused large losses in biodiversity due to narrow niches of tropical tree species (Bazzaz 1998, Miles et al. 2004). Those findings suggest higher vulnerability of tropical forests to climate change than previously believed (Lewis 2006, Corlett 2011).

Of particular concern associated with climate change in tropical forests are potential increases in tree mortality. The increased mortality is probably due to climate-induced physiological stress and interactions with climate-mediated disturbances such as insect outbreaks and wildfires, most notably in the Amazon rainforest (Huntingford et al. 2008, Malhi et al. 2009, Poulter et al. 2010, Good et al. 2011). Coupled climate-C models have also predicted that tropical forests would encounter a substantial and rapid 'dieback' or savannization by the end of the 21st century, especially in the Eastern Amazon rainforests (Cox et al. 2004, 2013, Scholze et al. 2006, Huntingford et al. 2008, Poulter et al. 2010), triggering a positive feedback from the terrestrial C cycle to climate warming (Friedlingstein et al. 2006). The positive climate-C feedbacks could accelerate loss of tropical rainforests (Betts et al. 2004). However, the projected dieback and the modeled positive feedbacks are largely based on relatively simple response functions, which lack functionally realistic mortality mechanisms (Allen et al. 2010). Those functions mostly derive from leaf-level physiology but have not been carefully tested against experimental results at the forest-stand level.

Predicting the consequences of climate change on tropical forests has emerged as one of the grand challenges for global change scientists. If the responses and feedbacks of tropical forests to climate change are not adequately addressed, it is difficult to gauge myriad mitigation strategies and to develop adaptive approaches to alleviate climate change. Gaining such an understanding will require an international framework of global change research networks to assess climate-ecosystem feedbacks. In this essay, we first review atmospheric and climatic changes in the tropics and their impacts that have been observed on tropical forests from various complementary approaches and global change research (Figure 1). Secondly, we discuss the need for large-scale manipulative experiments in tropical forests and some of the key questions that such experiments can potentially answer. In the last section, we briefly discuss the technical, logistical and financial challenges for the proposed experiments. Our discussion is focused primarily on tropical rainforests, or moist, wet or humid tropical forests in regions where the mean temperature of the coldest month is  $>18^{\circ}\text{C}$  and the monthly rainfall is  $>100\text{ mm}$  (Whitmore 1998).

### Atmospheric and climatic changes in the tropics

In tropical forest regions, the atmospheric  $\text{CO}_2$  concentration follows the global trend, which increased by 1.66 ppm or

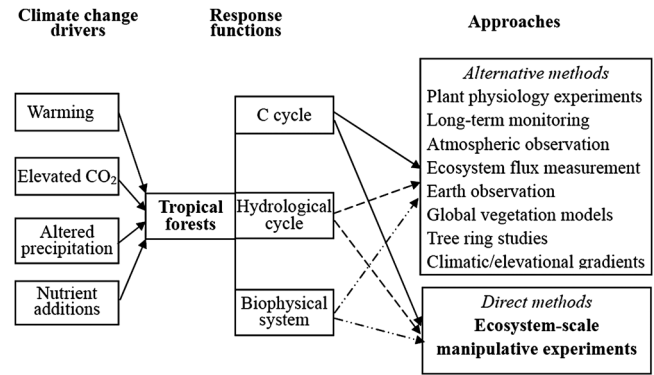


Figure 1. Methods used to examine the effects of climate change on the C cycle, the hydrological cycle and the biophysical cycle in tropical forests.

0.46% year<sup>-1</sup> from 1980 to 2007 (totally 44.8 ppm; Keeling and Whorf 2008). The mean rate of tropical warming between 1976 and 1998 was  $0.26 \pm 0.05^{\circ}\text{C}$  per decade (Malhi and Wright 2004), which was comparable to the global mean land surface temperature rise of  $0.22 \pm 0.08^{\circ}\text{C}$  per decade between 1976 and 2000 (IPCC 2007). The recent warming is strongest in the extratropics of the northern hemisphere with large El Niño events (IPCC 2007). Global climate models have predicted that all tropical forest regions would encounter a further warming of between 3 and 6 °C (mean) by the end of this century, which will move outside the range of natural variability of at least the past 2 million years (Cramer et al. 2004, Zelazowski et al. 2011). From 1976 to 1998, precipitation has decreased in tropical forest regions at a rate of  $1.0 \pm 0.8\%$  per decade, with large spatial variability. It decreased more significantly in northern tropical Africa (3–4% per decade) but did not change in Amazonia (Malhi and Wright 2004). Droughts have become more common since the 1970s. Future changes in spatial rainfall patterns are expected to be highly variable over space, with changes of up to  $\pm 20\%$  by 2100 (Malhi et al. 2009, Zelazowski et al. 2011). A consistent rise in precipitation has been predicted to occur in Asian tropical forest regions (Cramer et al. 2004). Although atmospheric nitrogen (N) deposition has mostly occurred in temperate regions due to local sources and the short lifespan of  $\text{NO}_x$  and  $\text{NH}_3$  in the atmosphere, N deposition rates in the tropics have also been found to increase over recent decades and are expected to substantially increase far beyond those experienced for millions of years (Galloway et al. 2008, Davidson 2009).

### What we learn about tropical forests from various approaches

It is very difficult to conduct ecosystem-scale experiments to reveal fundamental mechanisms underlying forest responses to climate change in tropical regions due to their operational difficulties in such high-stature tropical forests. Rather, a

diverse array of other methods has been employed to understand possible responses of tropical forests to global environmental change. Those methods include long-term monitoring, plant physiology experiments, atmospheric observation, ecosystem flux measurement, Earth observation, modeling, tree ring studies and studies along climatic or elevational gradients (Figure 1). Lewis et al. (2009a) have carefully discussed the first six of these approaches. In this section, we briefly summarize the findings of those, and discuss the last two methods in more detail in the context of our argument for ecosystem-scale manipulative experiments.

To date, much attention has been paid to observation in long-term monitoring plots, but the results have been conflicting. For example, tropical tree growth rates increased significantly over the last several decades in tropical Amazonia and Africa (Phillips et al. 2004, Lewis et al. 2009b), but were negatively affected by subtle increases in average temperature in Central America and Asia (Clark et al. 2003, Feeley et al. 2007). Plant C storage, tree mortality and recruitment, liana change and stem dynamics also showed inconsistent responses to environmental change over time (Baker et al. 2004, Lewis et al. 2009b). The differences may partly result from different measuring intervals, with 5–10 years in Amazonia/Africa and 1–5 years in Central America/Asia. Similarly, results from both ecosystem flux measurements and atmospheric observations showed that tropical forests were either a C sink, a C source or in balance, probably due to measurement failure on calm nights and high uncertainty in CO<sub>2</sub> sampling and atmospheric transport models, respectively (Grace et al. 1995, Malhi et al. 1998, Lewis et al. 2009a). Nevertheless, plant physiology experiments, Earth observation and modeling indicate increased trends in plant photosynthesis, productivity and C storage over time (Lewis et al. 2009a).

Tree ring studies allow us to reconstruct annual growth rates over the full lifetime of tropical trees (Zuidema et al. 2012). The results showed an increase in the long-term growth rates for several Amazonian species (Rozendaal et al. 2010), but not for Asian species (Nock et al. 2011). Climatic or elevational gradients as a proxy for future climate change have been used to examine long-term responses of ecosystem processes. An increased trend in aboveground NPP has often been found across a temperature or precipitation transect gradient when precipitation is <3500 mm (Austin 2002). Along elevational gradients, a 5 °C warming causes loss of ~30% of epiphyte species and nearly 80% of ant species in Costa Rica (Colwell et al. 2008, Wright et al. 2009).

All of the above-mentioned tropical forest–climate studies are based on correlative approaches that link ecosystem attributes with climate variables using observation data. For example, in plant physiology studies, the respiration–temperature relationship is commonly described as an exponential function with a temperature sensitivity coefficient, known as  $Q_{10}$

(a relative increase in respiration rate for every 10 °C increase in temperature), to interpret the effects of climate warming (Lloyd and Farquhar 2008). In long-term monitoring plots, changes in mean annual temperature are often used, together with the temperature sensitivity function, to examine the effects of warming on ecosystem structure and function (Lewis et al. 2009b, Phillips et al. 2009). Such extrapolation ignores various ecosystem-scale processes and often results in uncertainty in prediction. Overall, these approaches may offer valuable insights into climatic impacts on tropical forests, while multiple climatic and biotic factors may confound the effects, making it difficult to detect fundamental mechanisms underlying ecosystem responses and feedbacks to climate change.

### What we know about ecosystem responses from global change research

Large-scale manipulative experiments have been conducted in temperate forests to examine ecosystem responses to elevated CO<sub>2</sub> (e.g., King et al. 2004, Norby et al. 2010), soil warming (Melillo et al. 2002), drought (Yavitt and Wright 2001, Borken et al. 2006, Pérez-Ramos et al. 2010) and N deposition (Janssens et al. 2010, Lu et al. 2011). Those experiments have advanced our knowledge about climate effects on forests in temperate regions (Rustad et al. 2001, Field et al. 2007, Luo 2007). In tropical forests, studies have been conducted to examine ecosystem responses to altered precipitation by throughfall exclusion experiments and N deposition (e.g., Yavitt and Wright 2001, Lohse and Matson 2005, Davidson et al. 2008). While no ecosystem-scale manipulative experiment has been conducted with rising CO<sub>2</sub> and warming (Körner 2009, Lewis et al. 2009a), the effects of elevated CO<sub>2</sub> and warming have been examined from greenhouse and mesocosm experiments. Here, we synthesize results from various experiments to evaluate main and interactive effects of various global change drivers (e.g., elevated CO<sub>2</sub>, altered precipitation, warming and N deposition) on ecosystem processes, from which we try to derive insights into potential responses of tropical forests to global change.

#### Elevated atmospheric CO<sub>2</sub> concentration

Although no single mature tropical tree has even been exposed to a CO<sub>2</sub>-enriched atmosphere, several studies have examined ecophysiological responses to elevated CO<sub>2</sub> with seedlings, young saplings and model communities grown in enclosures (see Körner 2009 for details). In general, elevated CO<sub>2</sub> consistently stimulated leaf photosynthesis but either increased or showed no change in forest productivity (Arnone and Körner 1995, Lovelock et al. 1998). A positive photosynthetic response of tropical leaves to elevated CO<sub>2</sub> thus cannot necessarily be scaled up to whole trees. In addition, modeling may result in overestimation of elevated CO<sub>2</sub> effects on tropical

forests if the canopy was treated as a big leaf to simulate fluxes of CO<sub>2</sub> and water vapor (Dai et al. 2004).

### Altered precipitation

The most significant threat to tropical forests probably results from drought and changes in rainfall patterns (Bawa and Markham 1995). Several large-scale throughfall exclusion experiments have been conducted in the Brazilian Amazon and southwestern Costa Rica. The results showed that drought consistently decreased aboveground NPP and root growth, and increased mortality of large trees and lianas (Cattanio et al. 2002, Nepstad et al. 2007, Brando et al. 2008). Less consistent were responses of soil greenhouse gas emissions (GHGs, i.e., CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>O and NO) to drought in different sites (Cattanio et al. 2002, Sotta et al. 2007, Davidson et al. 2008, Cleveland et al. 2010). Moreover, global models predicted the possibility of increased precipitation in some tropical regions (IPCC 2007). Irrigation experiments have also been carried out in Barro Colorado Island Panama and southeastern Amazonian Peru (Wieder and Wright 1995, Yavitt and Wright 2001, Bunker and Carson 2005, Paine et al. 2009). Irrigation significantly enhanced young seedling growth and survival, increased stem density and diversity (Bunker and Carson 2005, Paine et al. 2009) and stimulated litter decomposition on forest floors (Wieder and Wright 1995). No effects were observed on fine root biomass (Yavitt and Wright 2001). These studies have largely improved our understanding on process responses to altered precipitation in tropical forests in comparison with observational studies that have the co-occurrence of multiple factors (Clark 2004).

### Climate warming

The potential effects of climate warming on tropical forests are increasingly becoming a focus of climate change research. No large-scale warming experiments have been conducted in mature tropical forests, not even in soil using buried electric resistance wires or sub-canopy with infrared heaters, which have been applied in temperate forests (e.g., Melillo et al. 2002, Schindlbacher et al. 2009, Reich 2010). The only in situ warming experiment was to date carried out on leaves and branches of mature trees, lianas and gap species using electric resistance heaters in the Amazon (Doughty 2011). It was found that warming decreased maximum photosynthesis ( $A_{max}$ ), with a larger negative impact on mature trees than on lianas or gap species, but did not affect transpiration (Doughty 2011). Whole-ecosystem warming experiments are limited only to low-stature grasslands to date (e.g., Shaver et al. 2000, Luo et al. 2001, Niu et al. 2011). It is commonly assumed that tropical forests may be largely unaffected in comparison with boreal forests due to less warming near the equator than close to the poles (Markham 1998). However, tropical trees are more susceptible to climate warming than temperate or boreal plants

due to narrow diurnal, annual and interannual temperature tolerance ranges (Hoffmann 2010). Furthermore, tropical forests are thought already to be close to their high-temperature threshold (Doughty and Goulden 2008) and their response to climate warming will depend on their ability to acclimate (Way and Oren 2010).

### Nitrogen deposition

Owing to easy implementation, N deposition experiments have been conducted in the tropical forests of Brazil, Costa Rica, Hawaii, USA, Panama and Puerto Rico (Wieder and Wright 1995, Lohse and Matson 2005, Siddique et al. 2010, Adamek et al. 2011). Nitrogen addition significantly increased aboveground biomass (Adamek et al. 2009, Cusack et al. 2011), but its effects on fine root biomass were not directional with either decreases (Cusack et al. 2011) or no changes (Li et al. 2006, Adamek et al. 2011) observed. A meta-analysis showed that N addition increased litter biomass and did not significantly affect soil and microbial respiration, soil C content, dissolved organic C and microbial biomass C (Liu and Greaver 2010). Nitrogen enrichment can also decrease species richness of the understorey plants (Bobbink et al. 2010).

### Potential interactions of multiple drivers

In the real world, global climate change usually involves simultaneous changes in the above-mentioned drivers (IPCC 2007), which interactively affects ecosystem processes (Norby and Luo 2004). Multi-factor manipulative experiments may cause dramatic shifts in ecosystem C dynamics relative to the single-factor ones due to additive, synergic and antagonistic effects (Zhou et al. 2006, Heimann and Reichstein 2008, Lin et al. 2010). For example, seedlings of nine tropical forest tree species showed strong growth stimulation by elevated CO<sub>2</sub> when N addition was applied (Winter and Lovelock 1999), while CO<sub>2</sub> effects were not clear in the absence of fertilizer (Lovelock et al. 1998, Winter et al. 2000). Modeling interactive efforts can provide understanding of long-term dynamics to inform future multi-factor experiments (Luo et al. 2008). Such efforts have indicated that the temperature threshold of NPP decreased with increasing precipitation in Amazonian tropical rainforests (Cowling and Shin 2006).

### The need for large-scale manipulative experiments in tropical regions

Large-scale manipulative experiments can play an indispensable role in probing mechanisms underlying tropical forest responses to future climate, especially elevated CO<sub>2</sub> and warming and their interaction (Körner 2009, Lewis et al. 2009a, Corlett 2011). By manipulating one or a few global change factors, the experiments can quantify direct and indirect effects of the factors on various ecosystem processes.

The experimental approaches can minimize the confounding effects that are difficult to avoid in observational approaches (Figure 1). Although we have gained much knowledge from global change experiments in temperate regions, direct extrapolation of such knowledge to tropical regions may not be warranted due to their unique ecosystem attributes. The global change experiments conducted in tropical regions can help integrate our knowledge gained from study of the aboveground processes alone (Phillips et al. 1998, 2009, Clark et al. 2003) and aid investigation of the linkage between canopy and soil processes.

The most challenging experiments that need to be conducted in tropical forests are warming and CO<sub>2</sub> manipulations. Although current approaches for elevated CO<sub>2</sub> (FACE) are available in temperate forests, further modifications are still needed to allow experiments to be conducted in such tall-stature systems. For example, it is technically difficult to manage CO<sub>2</sub> gas flow at the required quantities to fumigate all the parts of the canopy. Warming experiments are even more difficult to manipulate in tropical forests. The difficulties—both conceptual and operational—increase if warming treatment is combined with elevated CO<sub>2</sub>. The current technological development may serve as a prototype using nested hexagonal and rectangular arrays of infrared heaters to increase forest temperatures uniformly from root to canopy (Kimball et al. 2011). Combined air and soil warming may also achieve the target levels of ecosystem warming (Hanson et al. 2011) when a forced-air heating system is used to warm large open-top chambers for aboveground plant space (Norby et al. 1997, Pelini et al. 2011) and buried heating cables or circumferential vertical heaters to warm soils (Melillo et al. 2002, Bronson and Gower 2010). The open-top chambers for air warming can be also used for CO<sub>2</sub> fumigation to examine their interactive effects. Alternatively, warming from infrared heaters may be combined with a FACE facility to elevate CO<sub>2</sub> for investigation of their interactive effects.

The level of experimentally manipulated factors can be decided in reference to model predictions from IPCC (2007), which may vary from 2 to 4 °C for rising temperature and 600–800 ppm for elevated CO<sub>2</sub>. If possible, N deposition treatment can be added to either warming or elevated CO<sub>2</sub> treatments. If the budget allows, it is better to have several such experiments in different tropical forest locations (or countries), since ecosystem responses to climate change may vary among diverse tropical ecosystems. For example, responses of GHGs to drought using throughfall exclusion experiments varied significantly in tropical forests (Cattanio et al. 2002, Sotta et al. 2007, Davidson et al. 2008, Cleveland et al. 2010). Those experiments can allow some of the key questions to be addressed as discussed below and will provide valuable platforms for probing mechanisms underlying vulnerability of tropical forests to climate change.

Most past research on climatic responses and feedbacks has mainly focused on the potential role of tropical forests as C sources or sinks (Field et al. 2007). However, it is commonly acknowledged that tropical forests influence global climate systems through multiple pathways, primarily by exchanges of biogeochemical, hydrological and biophysical fluxes with the atmosphere (Figure 2a; Bonan 2008, Chapin et al. 2008). For example, tropical forests receive a larger portion of solar energy in comparison with temperate and boreal regions, which drives evapotranspiration (ET) for tropical convection, atmospheric mixing and circulation, having downstream effects on temperate and boreal regions (Werth and Avissar 2004). Warming may increase ET and sensible heat flux, and then cloud cover in tropical regions, which may contribute to cooling by increasing ET from land to air as well as reflecting sunlight back to space (Figure 2c; Bonan 2008, Chapin et al. 2008, Jackson et al. 2008). Climate change may thus have different impacts on biogeochemical, hydrological and biophysical processes (Figure 2b and d; Bonan 2008), which can be examined in such proposed experiments from leaf to ecosystem scales.

Long-term ecological responses to global change are strongly regulated by slow processes, such as changes in species composition, C dynamics in soil, long-lived plants and accumulation of nutrient capitals (Clark and Clark 2011, Feeley et al. 2011, Luo et al. 2011). For example, liana abundance and biomass has increased significantly due to recent ongoing global change, which may affect tree diversity, recruitment, growth and survival, and subsequently C fluxes and storage (Schnitzer and Bongers 2011). To maximize their benefit to probe responses of long-term ecosystem processes, such experiments would need to be run for at least 10 years. The experimental size should be at least 20-m diameter ring or 20 × 20 m, owing to high biodiversity in tropical forests. Meanwhile, ecosystem models can help to integrate results from those experiments with other sources of information (Luo et al. 2011). With data assimilation, experimental data can inform the initial conditions and constrain model parameters to improve ecological forecasting and estimates of uncertainty in prediction of tropical forest responses to global change.

### Key questions to be answered by global change research

Global change experiments, if they are appropriately designed, could address some of the most critical issues in tropical ecosystems. We briefly discuss them as follows.

(i) How likely is climate change to induce Amazon forest dieback? Which factor, drought or warming, is most important in causing forest decline? Can warming and drought effects on tropical forests be ameliorated by elevated CO<sub>2</sub>? What is the capacity of tropical forests to adapt to climate change in the

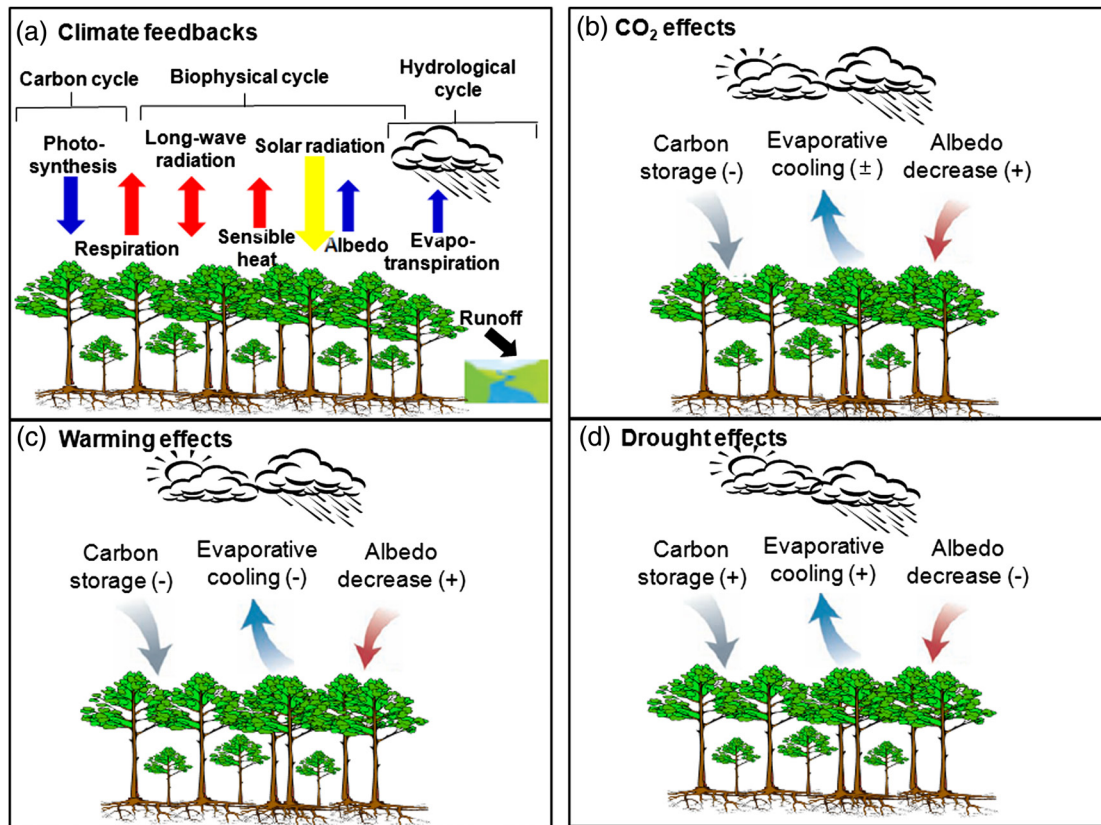


Figure 2. Climate feedbacks of the C cycle, the hydrological cycle and the biophysical cycle in tropical forests (a) and simplified effects of elevated CO<sub>2</sub> (b), warming (c) and drought (d) on climate feedbacks (modified from Chapin et al. (2008) for panel a). The C cycle includes CO<sub>2</sub> uptake by tropical rainforests (photosynthesis) and CO<sub>2</sub> loss to the atmosphere by respiration. The biophysical cycle encompasses incoming solar radiation, reflected proportions of incoming solar radiation (albedo), the absorbed radiation transferred to the atmosphere as sensible heat (warming the near-surface air), ET (cooling the surface) and long-wave radiation. The hydrological cycle includes rainfall input, ET and runoff. Cooling effects on climate are shown by blue arrows; warming effects by red arrows. Panels b, c and d show only the climate effects of C storage, evaporative cooling and albedo decrease. Symbols +, – and ± represent positive, negative and neutral feedbacks. Panel 2a is modified with permission from ESA journal, *Frontiers in Ecology and the Environment*: Chapin et al. (2008).

long term? Currently, the climate-induced forest dieback predicted by coupled climate-C models (especially in the Amazonian region; Cox et al. 2000, Huntingford et al. 2008, Poulter et al. 2010) is largely based on leaf- and plant-level physiology with two different, not necessarily exclusive, mechanisms: high-temperature inhibition of leaf photosynthetic uptake (Doughty and Goulden 2008) and increased respiratory losses that push trees into C starvation (McDowell et al. 2008). Since elevated CO<sub>2</sub> has been shown to increase water-use efficiency, this may compensate for drought conditions (Körner 2009). It would become possible to test this hypothesis if large-scale warming and elevated CO<sub>2</sub> experiments are constructed in tropical forests. In addition, the responses of tropical trees to warming and elevated CO<sub>2</sub> may be different among diverse species (Way and Oren 2010). Such experiments will help us to examine responses of individual dominant species to global change and contribute to our understanding of forest dieback in the tropics. If necessary, complementary small-scale experiments may need to coordinate with large-scale ones to evaluate specific mechanisms (Luo et al. 2011).

(ii) How important is it to represent accurately the processes of mortality or succession in dynamic global vegetation models (DGVMs) for predicting forest dieback or ‘savannization’? How does biodiversity regulate forest dieback under climate change? Despite the prominence with which simulated forest dieback and transition to savanna have motivated recent studies in tropical ecosystems, none of the DGVMs so far have actually incorporated key processes of mortality, recruitment and succession. The importance of this omission can be partly explored by comparing models that include these processes with experiments that actually show how mortality arises differentially under different treatment conditions.

(iii) What are the effects of elevated CO<sub>2</sub> on forest productivity and C balance? Does CO<sub>2</sub> fertilization of tropical forests contribute to the explanation of the missing C sink? Although elevated CO<sub>2</sub> has been shown to significantly increase leaf-level photosynthesis in seedlings and model communities, its effects on forest productivity at stand levels and on C sequestration in soil and ecosystems have only been simulated by models or speculated based on simple extrapolation (Lin

et al. 1998, Lloyd and Farquhar 2008, Körner 2009). Ecosystem-level experiments can provide direct evidence for responses of forest productivity and C balance to elevated CO<sub>2</sub> in tropical forests.

(iv) Will climate warming trigger tropical C-cycle feedback that leads to a warmer climate? In tropical regions, the majority of the models have simulated a decrease in NPP and net ecosystem productivity (NEP), because tropical NPP and NEP may be more moisture dependent (Friedlingstein et al. 2006). Both the direction and degree of the response of NPP and respiratory C release to climate warming remain largely uncertain in tropical forests. In many other regions of the globe, experimental warming has often been found to stimulate plant growth more than or equally to C loss (Luo 2007). Whether climate warming stimulates plant growth more or less than C loss in tropical forests can be addressed with manipulative experiments.

(v) How do biogeochemical, hydrological and biophysical processes respond to climate change in tropical forests? Fluxes between the ecosystems and the atmosphere are strongly coupled and are usually represented in DGVMs or individual-based models (e.g., ecosystem demography models) (Moorcroft et al. 2001, Sitch et al. 2008). However, calibration and validation are often difficult for hydrological and biophysical cycles, in particular, under climate change. The results from integrated studies of biogeochemical, hydrological and biophysical processes in large-scale experiments could be used to improve mathematical representations of tropical vegetation and better predict the response and feedbacks of future tropical forests to climate change.

### Moving forward: a strategy for manipulative experiments

Achieving an accurate assessment of climate–ecosystem feedback and forecasting the future climate system will require integrated ecosystem-level climate change studies. Conducting ecosystem-scale experiments, especially warming and/or elevated CO<sub>2</sub>, in natural tropical forests can advance science in this area but will pose many challenges in terms of technology, infrastructure, cost and multinational and multidisciplinary collaboration. Thus, success of such a research program will require an international framework to coordinate collaboration among nations, institutions and disciplines worldwide. The challenge of creating such a network demands integrated, multidisciplinary approaches and new thinking.

Assessing the sensitivity of tropical ecosystems to climate change and identifying key attributes would require an integrated approach to research planning and execution. It would be ideal to have multi-factor experiments with multiple levels of CO<sub>2</sub> concentration, warming, drought and nutrient additions for both primary and secondary tropical forests (Hanson et al.

2008). However, such experiments will require a considerable investment in site construction and maintenance costs, making them very expensive. For example, building either a FACE or a warming facility would cost several million dollars (Calfapietra et al. 2010, Kimball et al. 2011). Operational costs would be even more significant due to the requirements for large amounts of high quality CO<sub>2</sub> and electrical power for warming, as well as the engineers and scientific personnel among others. Ways to potentially achieve financial savings are thus necessary. To drastically reduce experimental costs, experimental sites may be close to an available CO<sub>2</sub> source such as a fertilizer plant (Calfapietra et al. 2010). Suggested locations are Brazil, Costa Rica, Puerto Rico, Northern Australia, Hawaii and Malaysia (Hanson et al. 2008). Most importantly in the Amazonian regions, experiments should preferably be associated with other studies (e.g., eddy flux-tower facilities).

Clearly, strategic planning is necessary to cope with organization, costs and the complexity of multi-dimensional datasets to address the most pressing scientific goals. Such tropical research needs precursor countries, with large research investments as well as a transcontinental support possibly funded by an international institution. To explore more deeply the establishment of ecosystem-level global change experiments in tropical forests, workshops are needed to develop ideas, solicit input from the community and nurture international collaborations.

### Conflict of interest

None declared.

### Funding

This research was financially supported by the National 'Thousand Young Talents' Program in China, the Program for Professor of Special Appointment (Eastern Scholar) at Shanghai Institutions of Higher Learning and 2012 Shanghai Pujiang Program (12PJ1401400), as well as by the US Department of Energy, Terrestrial Ecosystem Sciences grant DE SC0008270 and US National Science Foundation (NSF) grants DBI 0850290, EPS 0919466, DEB 0743778, DEB 0840964 and EF 1137293.

### References

- Adamek M, Corre MD, Holscher D (2009) Early effect of elevated nitrogen input on above-ground net primary production of a lower montane rain forest, Panama. *J Trop Ecol* 25:637–647.
- Adamek M, Corre MD, Hoelscher D (2011) Responses of fine roots to experimental nitrogen addition in a tropical lower montane rain forest, Panama. *J Trop Ecol* 27:73–81.
- Allen CD, Macalady AK, Chenchouni H et al. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manag* 259:660–684.

- Arnone JA, Körner C (1995) Soil and biomass carbon pools in model communities of tropical plants under elevated CO<sub>2</sub>. *Oecologia* 104:61–71.
- Austin AT (2002) Differential effects of precipitation on production and decomposition along a rainfall gradient in Hawaii. *Ecology* 83:328–338.
- Baker TR, Phillips OL, Malhi Y et al. (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob Change Biol* 10:545–562.
- Bawa KS, Markham A (1995) Climate-change and tropical forests. *Trends Ecol Evol* 10:348–349.
- Bazzaz FA (1998) Tropical forests in a future climate: changes in biological diversity and impact on the global carbon cycle. *Clim Change* 39:317–336.
- 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. *Theor Appl Climatol* 78:157–175.
- Bobbink R, Hicks K, Galloway J et al. (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol Appl* 20:30–59.
- Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444–1449.
- Borken W, Savage K, Davidson EA, Trumbore SE (2006) Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. *Glob Change Biol* 12:177–193.
- Brando PM, Nepstad DC, Davidson EA, Trumbore SE, Ray D, Camargo P (2008) Drought effects on litterfall, wood production and below-ground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. *Philos Trans R Soc B Biol Sci* 363:1839–1848.
- Bronson DR, Gower ST (2010) Ecosystem warming does not affect photosynthesis or aboveground autotrophic respiration for boreal black spruce. *Tree Physiol* 30:441–449.
- Bunker DE, Carson WP (2005) Drought stress and tropical forest woody seedlings: effect on community structure and composition. *J Ecol* 93:794–806.
- Calfapietra C, Ainsworth EA, Beier C et al. (2010) Challenges in elevated CO<sub>2</sub> experiments on forests. *Trends Plant Sci* 15:5–10.
- Cattanio JH, Davidson EA, Nepstad DC, Verchot LV, Ackerman IL (2002) Unexpected results of a pilot throughfall exclusion experiment on soil emissions of CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>O, and NO in eastern Amazonia. *Biol Fertil Soils* 36:102–108.
- Chapin FS, Randerson JT, McGuire AD, Foley JA, Field CB (2008) Changing feedbacks in the climate-biosphere system. *Front Ecol Environ* 6:313–320.
- Clark DA (2004) Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. *Philos Trans R Soc Lond B Biol Sci* 359:477–491.
- Clark DA, Clark DB (2011) Assessing tropical forests' climatic sensitivities with long-term data. *Biotropica* 43:31–40.
- Clark DA, Piper SC, Keeling CD, Clark DB (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proc Natl Acad Sci USA* 100:5852–5857.
- Cleveland CC, Wieder WR, Reed SC, Townsend AR (2010) Experimental drought in a tropical rain forest increases soil carbon dioxide losses to the atmosphere. *Ecology* 91:2313–2323.
- Cleveland CC, Townsend AR, Taylor P et al. (2011) Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. *Ecol Lett* 14:939–947.
- Colwell RK, Brehm G, Cardelus CL, Gilman AC, Longino JT (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258–261.
- Corlett RT (2011) Impacts of warming on tropical lowland rainforests. *Trends Ecol Evol* 26:606–613.
- Cowling SA, Shin Y (2006) Simulated ecosystem threshold responses to co-varying temperature, precipitation and atmospheric CO<sub>2</sub> within a region of Amazonia. *Glob Ecol Biogeogr* 15:553–566.
- 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.
- Cox PM, Betts RA, Collins M, Harris PP, Huntingford C, Jones CD (2004) Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theor Appl Climatol* 78:137–156.
- Cox PM, Pearson D, Booth BB, Friedlingstein P, Huntingford C, Jones CD, Luke CM (2013) Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* 494:341–344.
- Cramer W, Bondeau A, Schaphoff S, Lucht W, Smith B, Sitch S (2004) Tropical forests and the global carbon cycle: impacts of atmospheric carbon dioxide, climate change and rate of deforestation. *Philos Trans R Soc Lond B Biol Sci* 359:331–343.
- Cusack DF, Silver WL, Torn MS, McDowell WH (2011) Effects of nitrogen additions on above- and belowground carbon dynamics in two tropical forests. *Biogeochemistry* 104:203–225.
- Dai YJ, Dickinson RE, Wang YP (2004) A two-big-leaf model for canopy temperature, photosynthesis, and stomatal conductance. *J Clim* 17:2281–2299.
- Davidson EA (2009) The contribution of manure and fertilizer nitrogen to atmospheric nitrous oxide since 1860. *Nat Geosci* 2:659–662.
- Davidson EA, Nepstad DC, Ishida FY, Brando PM (2008) Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. *Glob Change Biol* 14:2582–2590.
- Dirzo R, Raven PH (2003) Global state of biodiversity and loss. *Annu Rev Environ Resour* 28:137–167.
- Doughty CE (2011) An in situ leaf and branch warming experiment in the Amazon. *Biotropica* 43:658–665.
- Doughty CE, Goulden ML (2008) Are tropical forests near a high temperature threshold? *J Geophys Res Biogeosci* 113, G00B07, doi:10.1029/2007JG000632.
- Feeley KJ, Wright SJ, Supardi MNN, Kassim AR, Davies SJ (2007) Decelerating growth in tropical forest trees. *Ecol Lett* 10:461–469.
- Feeley KJ, Davies SJ, Perez R, Hubbell SP, Foster RB (2011) Directional changes in the species composition of a tropical forest. *Ecology* 92:871–882.
- Field CB, Lobell DB, Peters HA, Chiariello NR (2007) Feedbacks of terrestrial ecosystems to climate change. *Annu Rev Environ Resour* 32:1–29.
- Foley JA, DeFries R, Asner GP et al. (2005) Global consequences of land use. *Science* 309:570–574.
- Friedlingstein P, Cox P, Betts R et al. (2006) Climate-carbon cycle feedback analysis: results from the (CMIP)-M-4 model intercomparison. *J Clim* 19:3337–3353.
- Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai Z, Freney JR, Martinelli LA, Seitzinger SP, Sutton MA (2008) Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* 320:889–892.
- Good P, Jones C, Lowe J, Betts R, Booth B, Huntingford C (2011) Quantifying environmental drivers of future tropical forest extent. *J Clim* 24:1337–1349.
- Grace J, Lloyd J, McIntyre J et al. (1995) Carbon-dioxide uptake by an undisturbed tropical rain-forest in southwest Amazonia, 1992 to 1993. *Science* 270:778–780.
- Hanson PJ, Classen AT, Kueppers L et al. (2008) Ecosystem experiments: understanding climate change impacts on ecosystems and feedbacks to the physical climate. Report of the workshop on Exploring Science Needs for the Next Generation of Climate Change and Elevated-CO<sub>2</sub> Experiments in Terrestrial Ecosystems. Department of Energy, Arlington, VA.



- Hanson PJ, Kolka RK, Norby RJ et al. (2011) Evaluating spruce-peatland responses under climatic and environmental change using an in situ field manipulation. In: American Geophysical Union, Fall Meeting 2010, San Francisco, CA, USA, abstract #B21A-0293.
- Hassan R, Scholes RJ, Ash N (2005) Ecosystems and human well-being: current state and trends. Island Press, Washington, DC.
- Heimann M, Reichstein M (2008) Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature* 451:289–292.
- Hoffmann AA (2010) Physiological climatic limits in *Drosophila*: patterns and implications. *J Exp Biol* 213:870–880.
- Huntingford C, Fisher RA, Mercado L et al. (2008) Towards quantifying uncertainty in predictions of Amazon 'dieback'. *Philos Trans R Soc B Biol Sci* 363:1857–1864.
- IPCC (2007) Climate change 2007: the physical science basis. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M and Miller HL (eds) Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Jackson RB, Randerson JT, Canadell JG et al. (2008) Protecting climate with forests. *Environ Res Lett* 3:1–5.
- Janssens IA, Dieleman W, Luyssaert S et al. (2010) Reduction of forest soil respiration in response to nitrogen deposition. *Nat Geosci* 3:315–322.
- Keeling CD, Whorf TP (2008) Atmospheric CO<sub>2</sub> records from sites in the SIO sampling network. In: Trends: A compendium of data on global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, TN.
- Kimball BA, Conley MM, Lewin KF (2011) Performance and energy costs associated with scaling infrared heater arrays for warming field plots from 1 to 100 m. *Theor Appl Climatol* 108:247–265.
- King JS, Hanson PJ, Bernhardt E, DeAngelis P, Norby RJ, Pregitzer KS (2004) A multiyear synthesis of soil respiration responses to elevated atmospheric CO<sub>2</sub> from four forest FACE experiments. *Glob Change Biol* 10:1027–1042.
- Körner C (2009) Responses of humid tropical trees to rising CO<sub>2</sub>. *Annu Rev Ecol Evol Systemat* 40:61–79.
- Lewis SL (2006) Tropical forests and the changing earth system. *Philos Trans Roy Soc B Biol Sci* 361:195–210.
- Lewis SL, Lloyd J, Sitch S, Mitchard ETA, Laurance WF (2009a) Changing ecology of tropical forests: evidence and drivers. *Annu Rev Ecol Evol Systemat* 40:529–549.
- Lewis SL, Lopez-Gonzalez G, Sonke B et al. (2009b) Increasing carbon storage in intact African tropical forests. *Nature* 457:1003–1006.
- Li YQ, Xu M, Zou XM (2006) Effects of nutrient additions on ecosystem carbon cycle in a Puerto Rican tropical wet forest. *Glob Change Biol* 12:284–293.
- Lin D, Xia J, Wan S (2010) Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. *New Phytol* 188:187–198.
- Lin GH, Marino BDV, Wei YD, Adams J, Tubiello F, Berry JA (1998) An experimental and modeling study of responses in ecosystems carbon exchanges to increasing CO<sub>2</sub> concentrations using a tropical rainforest mesocosm. *Aust J Plant Physiol* 25:547–556.
- Liu LL, Greaver TL (2010) A global perspective on belowground carbon dynamics under nitrogen enrichment. *Ecol Lett* 13:819–828.
- Lloyd J, Farquhar GD (2008) Effects of rising temperatures and [CO<sub>2</sub>] on the physiology of tropical forest trees. *Philos Trans R Soc B Biol Sci* 363:1811–1817.
- Lohse KA, Matson P (2005) Consequences of nitrogen additions for soil losses from wet tropical forests. *Ecol Appl* 15:1629–1648.
- Lovelock CE, Winter K, Mersits R, Popp M (1998) Responses of communities of tropical tree species to elevated CO<sub>2</sub> in a forest clearing. *Oecologia* 116:207–218.
- Lu M, Zhou XH, Luo Y, Yang Y, Fang YT, Chen J, Li B (2011) Minor stimulation of soil carbon storage by nitrogen addition: a meta-analysis. *Agric Ecosyst Environ* 140:234–244.
- Luo YQ (2007) Terrestrial carbon-cycle feedback to climate warming. *Annu Rev Ecol Evol Systemat* 38:683–712.
- Luo YQ, Wan SQ, Hui DF, Wallace LL (2001) Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413:622–625.
- Luo Y, Gerten D, Le Maire G et al. (2008) Modeled interactive effects of precipitation, temperature, and CO<sub>2</sub> on ecosystem carbon and water dynamics in different climatic zones. *Glob Change Biol* 14:1986–1999.
- Luo Y, Melillo J, Niu SL et al. (2011) Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Glob Change Biol* 17:843–854.
- Malhi Y, Wright J (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philos Trans R Soc Lond B Biol Sci* 359:311–329.
- Malhi Y, Nobre AD, Grace J, Kruijt B, Pereira MGP, Culf A, Scott S (1998) Carbon dioxide transfer over a central Amazonian rain forest. *J Geophys Res Atmos* 103:31593–31612.
- Malhi Y, Aragao LEOC, Galbraith D, Huntingford C, Fisher R, Zelazowski P, Sitch S, McSweeney C, Meir P (2009) Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proc Natl Acad Sci USA* 106:20610–20615.
- Markham A (1998) Potential impacts of climate change on tropical forest ecosystems. *Clim Change* 39:141–143.
- McDowell N, Pockman WT, Allen CD et al. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 178:719–739.
- Melillo JM, Steudler PA, Aber JD et al. (2002) Soil warming and carbon-cycle feedbacks to the climate system. *Science* 298:2173–2176.
- Miles L, Grainger A, Phillips O (2004) The impact of global climate change on tropical forest biodiversity in Amazonia. *Glob Ecol Biogeogr* 13:553–565.
- Moorcroft PR, Hurtt GC, Pacala SW (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecol Monogr* 71:557–585.
- 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.
- Niu S, Xing X, Zhang Z, Xia J, Zhou X, Song B, Li L, Wan S (2011) Water-use efficiency in response to climate change: from leaf to ecosystem in a temperate steppe. *Glob Change Biol* 17:1073–1082.
- Nock CA, Baker PJ, Wanek W, Leis A, Grabner M, Bunyavejchewin S, Hietz P (2011) Long-term increases in intrinsic water-use efficiency do not lead to increased stem growth in a tropical monsoon forest in western Thailand. *Glob Change Biol* 17:1049–1063.
- Norby RJ, Luo YQ (2004) Evaluating ecosystem responses to rising atmospheric CO<sub>2</sub> and global warming in a multi-factor world. *New Phytol* 162:281–293.
- Norby RJ, Edwards NT, Riggs JS, Abner CH, Wullschleger SD, Gunderson CA (1997) Temperature-controlled open-top chambers for global change research. *Glob Change Biol* 3:259–267.
- Norby RJ, Warren JM, Iversen CM, Medlyn BE, McMurtrie RE (2010) CO<sub>2</sub> enhancement of forest productivity constrained by limited nitrogen availability. *Proc Natl Acad Sci USA* 107:19368–19373.
- Paine CET, Harms KE, Ramos J (2009) Supplemental irrigation increases seedling performance and diversity in a tropical forest. *J Trop Ecol* 25:171–180.
- Pan YD, Birdsey RA, Fang JY et al. (2011) A large and persistent carbon sink in the world's forests. *Science* 333:988–993.
- Pelini SL, Bowles FP, Ellison AM, Gotelli NJ, Sanders NJ, Dunn RR (2011) Heating up the forest: open-top chamber warming manipulation of arthropod communities at Harvard and Duke Forests. *Methods Ecol Evol* 2:534–540.
- Pérez-Ramos IM, Ourcival JM, Limousin JM, Rambal S (2010) Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. *Ecology* 91:3057–3068.

- Phillips OL, Malhi Y, Higuchi N et al. (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282:439–442.
- Phillips OL, Baker TR, Arroyo L et al. (2004) Pattern and process in Amazon tree turnover, 1976–2001. *Philos Trans R Soc Lond B Biol Sci* 359:381–407.
- Phillips OL, Aragao LEOC, Lewis SL et al. (2009) Drought sensitivity of the Amazon rainforest. *Science* 323:1344–1347.
- Poulter B, Hattermann F, Hawkins E, Zaehle S, Sitch S, Restrepo-Coupe N, Heyder U, Cramer W (2010) Robust dynamics of Amazon dieback to climate change with perturbed ecosystem model parameters. *Glob Change Biol* 16:2476–2495.
- Reich PB (2010) B4WARMED: boreal forest warming at an ecotone in danger. Flyer, University of Minnesota, Twin Cities.
- Rozendaal DMA, Brienen RJW, Soliz-Gamboa CC, Zuidema PA (2010) Tropical tree rings reveal preferential survival of fast-growing juveniles and increased juvenile growth rates over time. *New Phytol* 185:759–769.
- Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J; Gcte-News (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126:543–562.
- Schindlbacher A, Zechmeister-Boltenstern S, Jandl R (2009) Carbon losses due to soil warming: do autotrophic and heterotrophic soil respiration respond equally? *Glob Change Biol* 15:901–913.
- Schnitzer SA, Bongers F (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecol Lett* 14:397–406.
- Scholze M, Knorr W, Arnell NW, Prentice IC (2006) A climate-change risk analysis for world ecosystems. *Proc Natl Acad Sci USA* 103:13116–13120.
- Shaver GR, Canadell J, Chapin FS et al. (2000) Global warming and terrestrial ecosystems: a conceptual framework for analysis. *Bioscience* 50:871–882.
- Siddique I, Guimaraes Vieira IC, Schmidt S, Lamb D, Reis Carvalho CJ, Figueiredo RDO, Blomberg S, Davidson EA (2010) Nitrogen and phosphorus additions negatively affect tree species diversity in tropical forest regrowth trajectories. *Ecology* 91:2121–2131.
- Sitch S, Huntingford C, Gedney N et al. (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five dynamic global vegetation models (DGVMs). *Glob Change Biol* 14:2015–2039.
- Sotta ED, Veldkamp E, Schwendenmann L, Guimaraes BR, Paixao RK, Ruivo MDLP, Da Costa ACL, Meir P (2007) Effects of an induced drought on soil carbon dioxide (CO<sub>2</sub>) efflux and soil CO<sub>2</sub> production in an Eastern Amazonian rainforest, Brazil. *Glob Change Biol* 13:2218–2229.
- Way DA, Oren R (2010) Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiol* 30:669–688.
- Werth D, Avissar R (2004) The regional evapotranspiration of the Amazon. *J Hydrometeorol* 5:100–109.
- Whitmore TC (1998) An introduction to tropical rain forests. 2nd edn. Oxford University Press, Oxford.
- Wieder RK, Wright SJ (1995) Tropical forest litter dynamics and dry season irrigation on Barro-Colorado Island, Panama. *Ecology* 76:1971–1979.
- Winter K, Lovelock CE (1999) Growth responses of seedlings of early and late successional tropical forest trees to elevated atmospheric CO<sub>2</sub>. *Flora* 194:221–227.
- Winter K, Garcia M, Lovelock CE, Gottsberger R, Popp M (2000) Responses of model communities of two tropical tree species to elevated atmospheric CO<sub>2</sub>: growth on unfertilized soil. *Flora* 195:289–302.
- Wright SJ, Muller-Landau HC, Schipper J (2009) The future of tropical species on a warmer planet. *Conserv Biol* 23:1418–1426.
- Yavitt JB, Wright SJ (2001) Drought and irrigation effects on fine root dynamics in a tropical moist forest, Panama. *Biotropica* 33:421–434.
- Zelazowski P, Malhi Y, Huntingford C, Sitch S, Fisher JB (2011) Changes in the potential distribution of humid tropical forests on a warmer planet. *Philos Trans R Soc A Math Phys Eng Sci* 369:137–160.
- Zhou XH, Sherry RA, An Y, Wallace LL, Luo YQ (2006) Main and interactive effects of warming, clipping, and doubled precipitation on soil CO<sub>2</sub> efflux in a grassland ecosystem. *Glob Biogeochem Cycles* 20:GB1003, doi:10.1029/2005GB002526.
- Zuidema PA, Brienen RJW, Schoengart J (2012) Tropical forest warming: looking backwards for more insights. *Trends Ecol Evol* 27:193–194.