

Tropical forest carbon balance in a warmer world: a critical review spanning microbial- to ecosystem-scale processes

Tana E. Wood^{1,2,*}, Molly A. Cavaleri³ and Sasha C. Reed⁴

¹ *International Institute of Tropical Forestry, USDA Forest Service, Jardín Botánico Sur, 1201 Calle Ceiba, Río Piedras, PR 00926-1115, USA*

² *Department of Environmental Science, Policy & Management, University of California-Berkeley, 137 Mulford Hall #3114, Berkeley, CA 94720-3114, USA*

³ *School of Forest Resources & Environmental Science, Michigan Technological University, 1400 Townsend Dr., Houghton, MI 49931, USA*

⁴ *U.S. Geological Survey, Southwest Biological Science Center, 2290 S. West Resource Blvd, Moab, UT 84532, USA*

ABSTRACT

Tropical forests play a major role in regulating global carbon (C) fluxes and stocks, and even small changes to C cycling in this productive biome could dramatically affect atmospheric carbon dioxide (CO₂) concentrations. Temperature is expected to increase over all land surfaces in the future, yet we have a surprisingly poor understanding of how tropical forests will respond to this significant climatic change. Here we present a contemporary synthesis of the existing data and what they suggest about how tropical forests will respond to increasing temperatures. Our goals were to: (i) determine whether there is enough evidence to support the conclusion that increased temperature will affect tropical forest C balance; (ii) if there is sufficient evidence, determine what direction this effect will take; and, (iii) establish what steps should be taken to resolve the uncertainties surrounding tropical forest responses to increasing temperatures. We approach these questions from a mass-balance perspective and therefore focus primarily on the effects of temperature on inputs and outputs of C, spanning microbial- to ecosystem-scale responses. We found that, while there is the strong potential for temperature to affect processes related to C cycling and storage in tropical forests, a notable lack of data combined with the physical, biological and chemical diversity of the forests themselves make it difficult to resolve this issue with certainty. We suggest a variety of experimental approaches that could help elucidate how tropical forests will respond to warming, including large-scale *in situ* manipulation experiments, longer term field experiments, the incorporation of a range of scales in the investigation of warming effects (both spatial and temporal), as well as the inclusion of a diversity of tropical forest sites. Finally, we highlight areas of tropical forest research where notably few data are available, including temperature effects on: nutrient cycling, heterotrophic *versus* autotrophic respiration, thermal acclimation *versus* substrate limitation of plant and microbial communities, below-ground C allocation, species composition (plant and microbial), and the hydraulic architecture of roots. Whether or not tropical forests will become a source or a sink of C in a warmer world remains highly uncertain. Given the importance of these ecosystems to the global C budget, resolving this uncertainty is a primary research priority.

Key words: biogeochemical cycling, carbon flux, carbon stocks, climate change, ecosystem processes, global warming, temperature, temperature threshold, tipping point, tropical forest.

CONTENTS

I. Introduction	2
II. Ecosystem C balance	3
(1) Elevation gradients and cross-site comparisons	3
(2) Eddy covariance	3
(3) Coupled C-climate models	3

* Address for correspondence (Tel: 434-242-0881; Fax: 787-766-6263; E-mail: wood.tana@gmail.com).

(4) Field warming experiments	4
(5) Synthesis: temperature effects on net C balance	4
III. Above ground	4
(1) Growth and turnover rates	4
(2) Individual tree growth and morphology	5
(3) Whole-plant water use and hydraulic architecture	5
(4) Photosynthesis and stomatal conductance	6
(5) Respiration	7
(6) Biogenic volatile organic compound emission	7
(7) Synthesis: above-ground processes and drivers	8
IV. Below ground	8
(1) Litter and root production	8
(2) Heterotrophic soil respiration	8
(3) Abiotic effects of temperature on SOC	10
(4) Autotrophic soil respiration	10
(5) Synthesis: controls on below-ground C storage	10
V. Indirect controls on C balance	11
(1) Litterfall quality	11
(2) Soil nutrient availability	11
(3) Temperature interactions with water, CO ₂ and light	12
(4) Synthesis: indirect controls on C cycling	12
VI. Conclusions	12
VII. Acknowledgments	13
VIII. References	13

I. INTRODUCTION

More than any other biome, tropical forests dominate the global carbon (C) flux between the biosphere and the atmosphere (Saugier, Roy & Mooney, 2001). They account for 55% of forest biomass (Pan *et al.*, 2011) and one third of the world's soil C (Jobbagy & Jackson, 2000). Due to the size of tropical C fluxes and stocks, even a slight change in the uptake and storage of C in these ecosystems could have substantial consequences for the global C cycle and present large feedbacks to future climate [e.g. efflux of 1% of the tropical soil C pool \approx total annual anthropogenic carbon dioxide (CO₂) emissions; IPCC (2007)]. Despite the importance of tropical forests to global C cycling, we have little understanding of how this vast amount of C will respond to future environmental change. Consistently warm temperatures and low intra- and inter-annual variability in temperature have led many researchers to focus their efforts on changes in precipitation as the primary driver of climate-change effects. New evidence challenges this paradigm, suggesting the potential for a strong response of tropical forests to subtle increases in temperature (Lewis *et al.*, 2009a). Although controversial, these findings have reopened the debate as to the importance of temperature in tropical forested ecosystems (Corlett, 2011; Reed, Wood & Cavaleri, 2012).

Climatic conditions in the tropics are more diverse than anywhere else in the world (Brown & Lugo, 1982). According to the Holdridge Life Zone System, 66 of the world's 116 life zones are found in the tropics, 30 of which support forests ranging from lowland dry deciduous to montane wet evergreen (Holdridge, 1967; Brown & Lugo, 1982). Across

tropical forests, mean annual temperature (MAT) can range from 10 to 28 °C, and mean annual precipitation (MAP) from 1000 to 6000 mm (Raich *et al.*, 2006; FAO, 2009). These differences in climate, as well as in other factors such as soil type, have led to an incredible level of diversity in community composition and forest structure, both within and among tropical forest sites. As such, tropical forests are unlikely to exhibit a single response trajectory to a changing climate.

Global models project mean temperature increases in the tropics that are either in line with the global mean (1.7–3.9 °C) or warmer (1.8–5.0 °C) (A1B Scenario; Christensen *et al.*, 2007). In contrast to the common perception that high-latitude areas face the most accelerated warming, recent work suggests that tropical systems are likely to shift to an unprecedented heat regime within the next two decades, where historical temperature extremes will become the norm (Christensen *et al.*, 2007; Anderson, 2011; Diffenbaugh & Scherer, 2011). These recent predictions place tropical systems as top-priority research biomes for ecosystem-scale climate change research (Luo *et al.*, 2011).

Here, we evaluate available data to ask three questions. First, is there enough evidence to support the conclusion that increased temperature will affect the tropical forest C balance? Second, if there is sufficient evidence, what direction will this effect take? Third, what steps can we take to resolve uncertainty surrounding tropical forest responses to increasing temperature? Given the broad scope of this topic, we place certain constraints on this review. First, we use a mass-balance approach by focusing primarily on the effects of temperature on inputs and outputs of C on hourly to decadal time scales and spanning microbial- to ecosystem-scale

responses. Next, due to their predominance in the tropics (i.e. 88% of all tropical forests; FAO, 2009), we concentrate on the responses of lowland tropical forests, which are at the warm end of the temperature spectrum with MATs $>20^{\circ}\text{C}$. In addition, temperature is likely to interact with other abiotic variables such as precipitation, atmospheric CO_2 concentration and light availability. Understanding the effects of multiple drivers simultaneously is clearly important; however, we currently lack the data to do so effectively. Therefore, we focus on temperature as an individual driver, independent of other abiotic variables. Finally, we limit the review to intact forests and exclude discussion of potential longer term shifts in forest community composition. Although both disturbance and changes in species composition are likely to be highly influential in determining tropical ecosystem C balance (Laurance, 1999; Enquist, 2002; Phillips *et al.*, 2002; Wright, 2005), a thorough examination of these topics is beyond the scope of this review.

II. ECOSYSTEM C BALANCE

Several approaches are used to evaluate the potential effects of warming on whole-ecosystem C balance, including: elevation gradients, cross-site comparisons, eddy covariance, coupled C-climate models, and field warming experiments. We explore current predictions of the tropical forest C balance response to increased temperature using these methodological approaches.

(1) Elevation gradients and cross-site comparisons

Temperature gradients within the tropics provide a valuable opportunity to assess the potential response of tropical forests to increased temperature by substituting space for time. Meta-analyses of the effects of temperature on C storage and fluxes across a broad range of tropical forest sites have found that total net primary production (NPP), litter production, tree growth, and below-ground C allocation all increase with increasing MAT (range = $10\text{--}28^{\circ}\text{C}$; Silver, 1998; Raich *et al.*, 2006) and the temperature to precipitation ratio (Brown & Lugo, 1982). However, soil C decomposition and turnover time also increase with increasing MAT, indicating that atmospheric C uptake *via* increased forest productivity could be offset by increased soil C loss with warming (Raich *et al.*, 2006). Although cross-site comparisons can provide a window into how tropical forest C balance might respond to increased temperature, they are not without limitations. Other environmental variables in addition to temperature vary along elevation gradients and among forest sites, including light availability and plant community composition, confounding the elucidation of single drivers and relationships. Cross-site comparisons also do not account for the consequences of perturbing a system away from its 'native' temperature. For example, a forest with a MAT of 24°C is likely not comparable to a forest with a MAT of 20°C after increasing temperature by 4°C . Tropical

communities develop over evolutionary time scales, and the rapid rate at which climate change is occurring may not enable sufficient time for these communities to adapt. Given that most tropical forests may be moving beyond temperatures historically experienced by these systems (Diffenbaugh & Scherer, 2011), there is high potential for tropical forests to surpass temperature thresholds. A temperature threshold/thermal optimum is defined as the maximum temperature for a given reaction or process, beyond which rates decline.

Tropical forests that maintain high MATs may be limited by factors other than temperature, such as nutrient availability (Townsend *et al.*, 2011). For example, if we restrict the meta-analyses by Raich *et al.* (2006) to sites with temperatures $>20^{\circ}\text{C}$, the relationships between temperature and tropical forest C stocks are no longer significant. Hence, while analyses of the C balance along temperature gradients within the tropics suggest that temperature may have little effect on the net C balance of tropical forests (Raich *et al.*, 2006), we cannot say with certainty that these trends will continue as the world continues to warm.

(2) Eddy covariance

Tower-based eddy covariance techniques can be used to correlate net ecosystem exchange (NEE) of CO_2 with temperature over large tracts of forest (500–100 ha). Eddy covariance data from the Brazilian Amazon combined with a simple gas-exchange model suggest that NEE is quite sensitive to temperature increases, and that the forest may switch from a C sink to a source with only a 1.2°C increase in MAT (Grace *et al.*, 1996). An Amazonian eddy covariance dataset over 1 year showed an overall trend of C source behaviour at temperatures above approximately 27°C (Doughty & Goulden, 2008), and a 3-year dataset from a rain forest in Costa Rica showed reduced C sink behaviour at air temperatures above 20°C (Loeschner *et al.*, 2003). Interestingly, a longer term (4 years) eddy covariance study in the Amazon found the strongest controls of the components of NEE to be phenology and light, rather than temperature (Hutyra *et al.*, 2007). Hence longer term data sets (3+ years) may be needed to predict accurately the consequences of warming for net C exchange in tropical forests.

(3) Coupled C-climate models

Models enable us to project the potential response of tropical forests to increased temperature over the next century. In contrast to most of the results discussed above, numerous atmosphere-biosphere modeling studies suggest that warmer tropical forests will likely become an increasing source of C to the atmosphere as a result of increased heterotrophic respiration (Cramer *et al.*, 2001), increased plant respiration (White, Cannell & Friend, 2000), decreased NPP or photosynthesis (White *et al.*, 2000; Cramer *et al.*, 2001), and/or forest dieback (White *et al.*, 2000). While there is general agreement among models that tropical forests are likely to become a net source of C as temperatures increase,

they disagree as to which variables are likely to control this response. Models are only as good as the available input data, however, and the lack of a mechanistic understanding of how tropical forests will respond to warming significantly constrains these endeavours.

(4) Field warming experiments

Field warming of both plants and soils provides a concomitant estimate of above- and below-ground responses to increased temperature, enabling a comprehensive analysis of the ecosystem warming response. Although a valuable tool for predicting temperature effects on ecosystem C balance, a large-scale warming experiment that incorporates both soils and the forest canopy does not currently exist for any forested ecosystem, due in large part to the challenges and expense of warming such a large area (Aronson & McNulty, 2009; Amthor *et al.*, 2010; Kimball, Conley & Lewin, 2011). Field experiments that measure temperature responses of individual components (e.g. soils) have been useful for evaluating the response of temperate forests to warming (e.g. Farnsworth *et al.*, 1995; Nakamura *et al.*, 2010; Melillo *et al.*, 2011); however, data from such experiments have yet to be published for the tropics.

(5) Synthesis: temperature effects on net C balance

Cross-site comparisons suggest that, over evolutionary time scales, an increase in forest NPP due to increased temperature

will offset increased soil C loss, with no net change in the C balance (Raich *et al.*, 2006). Coupled C-climate models and eddy covariance studies predict that tropical forests will become a net source of C; however, the models do not always agree as to which variables will drive the increased C loss, and eddy covariance results vary among studies. Resolving the potential effects of temperature on the net C balance of tropical forests will likely require an improved understanding of temperature controls on the flow of C into and out of the system over multiple time scales (Fig. 1). Carbon fluxes include, but are not limited to, temperature effects on net CO₂ uptake and release by plants, biomass turnover rates, biomass accrual, soil C inputs, decay rates, and mobilization of C stocks. Field warming experiments in the tropics would complement existing methodologies and would be incredibly valuable in elucidating these individual fluxes.

III. ABOVE GROUND

(1) Growth and turnover rates

Over the last several decades, long-term (5+ years) inventory plots in tropical forests around the globe have revealed contrasting trajectories of stand-level growth and biomass turnover. Datasets in tropical Africa and the Amazon have shown increasing growth rates (Phillips *et al.*, 2004; Lewis *et al.*, 2009b), while plots in Costa Rica, Panama, and Malaysia revealed decelerating growth (Clark *et al.*,

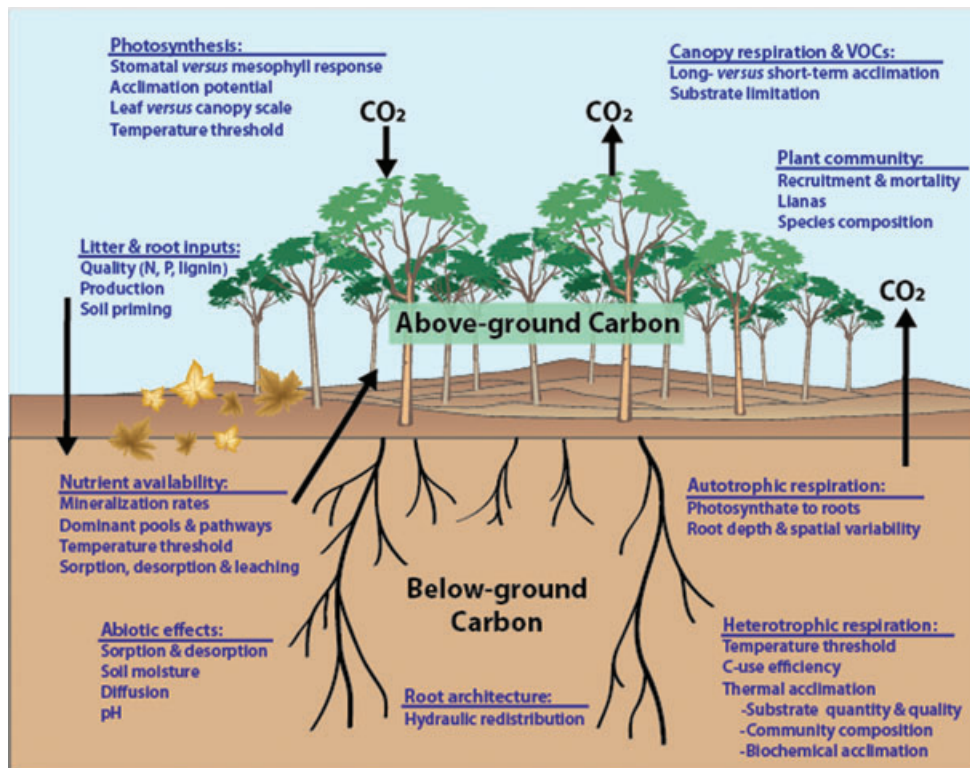


Fig. 1. Conceptual diagram of direct and indirect factors likely to affect the response of tropical forest C balance to increased temperature. VOCs, volatile organic compounds.

2003; Feeley *et al.*, 2007). A recent meta-analysis of large (16–52 ha), long-term tropical forest inventory plots across three continents (America, Africa and Asia) showed an increase in biomass over 20 years in seven of ten plots analyzed (Chave *et al.*, 2008). Both tree recruitment and mortality have also increased in Amazonian forests, with recruitment outpacing mortality (Phillips *et al.*, 2004). Possible drivers of increasing biomass increment include: CO₂ fertilization (Lloyd & Farquhar, 2008; Lewis *et al.*, 2009a), recovery from past disturbance (Chave *et al.*, 2008), or a shift in community composition towards faster growing species (Laurance *et al.*, 2004). Observed growth declines have been attributed to temperature-induced increases in plant respiration rates (Clark *et al.*, 2003; Feeley *et al.*, 2007); decreased net photosynthesis as a result of increasing temperature beyond the thermal optimum (Doughty & Goulden, 2008); or light limitation from increased liana shading of canopy trees, or from global dimming (Feeley *et al.*, 2007). Further evidence of a temperature effect on decreasing productivity includes increased mortality rates in several forests around the world during strong El Niño Southern Oscillation (ENSO) years, which exhibit higher temperatures and lower rainfall than normal years (Clark, 2004, and sources within). It is difficult to tease apart effects of temperature and precipitation when correlating growth to the large-scale climatic effects of ENSO, although temperature increases will likely coincide with lowered water availability through enhanced evapotranspiration rates. In a recent review, Clark (2004) focused on temperature increase as a major driver of tropical forest change, and suggested that as global temperatures increase tropical rain forests will likely show decreased productivity and increased mortality rates, thus shifting to a net C source.

(2) Individual tree growth and morphology

Tree ring analysis can be used to relate historical annual diameter growth to climatic variability. However, this methodology has limited application in tropical forests because few tropical trees develop annual growth rings, and even when present, tropical tree rings are usually the result of strong drought or dry season, making them difficult to interpret. Nevertheless, a 37-year tree ring record of a fast growing secondary forest tree species common to the dry forests of Mexico suggested that, although tree growth was related to temperature, dry-season rainfall was the primary driver of tree growth in this forest (Brienen *et al.*, 2010). This is not surprising given the degree of water limitation in this system, and highlights the difficulty in teasing apart individual climatic drivers with this technique.

Patterns of plant growth depend on the partitioning of photosynthate, but growth cannot always be predicted by rates of photosynthesis. Tropical forest species in Australia showed optimum growth under much higher temperatures than what was optimal for photosynthesis, indicating that growth can continue to increase even as photosynthesis declines with increasing temperature (Cunningham & Read, 2003a). Conversely, increased photosynthesis as a result of

elevated CO₂ in a mature tropical rain forest in Panama did not increase growth, but instead increased levels of non-structural carbohydrates in canopy tissue (Körner, 2003). Because source/sink feedbacks may have more control over tree C balance than either photosynthesis or respiration, a more mechanistic understanding of the response of tropical tree growth to increasing temperature should include investigating the effects of temperature on cell division and expansion (Ryan, 2010).

A recent global meta-analysis of the effects of temperature on tree growth found warming to increase foliage biomass, decrease root biomass, and produce taller, thinner stems, although tropical tree growth decreased overall when compared to either boreal or temperate species (Way & Oren, 2010). By contrast, a study of tropical tree seedlings in Australia showed increased root:shoot ratios under warming treatments (Cunningham & Read, 2003a). Warming may therefore alter the morphology and biomass allocation patterns of trees in addition to affecting diameter growth rate. As such, long-term studies (5+ years) in tropical forests showing growth patterns based solely on diameter may be misleading with respect to total biomass increment. Future studies in tropical forests should take into account the possible effects of warming on tree morphology and above- *versus* below-ground C allocation.

(3) Whole-plant water use and hydraulic architecture

Warming has the potential to alter the water balance of tropical forests, either by increasing or decreasing whole-plant transpiration, or by conferring competitive advantages to species with particular hydraulic architecture. In a Costa Rican tropical rain forest, sap flow was better correlated to vapour pressure deficit (VPD) than to soil moisture (O'Brien, Oberbauer & Clark, 2004), suggesting that transpiration may be more sensitive to changes in air temperature than to precipitation when soils are consistently moist (but see Williams *et al.*, 1998).

Tropical tree sap flow generally increases with increasing temperature (i.e. evaporative demand) up to a threshold, and then decreases as stomata close to maintain leaf water potential above a critical threshold (O'Brien *et al.*, 2004). Whole-canopy transpiration, however, depends upon both stomatal conductance and boundary layer conductance (Meinzer *et al.*, 1997). While stomatal conductance is primarily influenced by temperature, humidity, and solar radiation, boundary layer conductance is primarily driven by wind speed and leaf morphology (Meinzer *et al.*, 1997). As a result, global warming may affect stomatal conductance, but have little effect on boundary layer conductance, which may have greater influence than stomatal behaviour on whole-tree transpiration in tropical forest canopies (Meinzer *et al.*, 1997).

Hydraulic architecture may also have a strong effect on how species react to global climate change. Trees with shallow roots may be at a competitive disadvantage compared to deeper rooted species (Stork *et al.*, 2007). However, in a Panamanian tropical forest, Meinzer *et al.*

(1999) found that smaller trees tapped deeper water than larger trees. In Amazonian forest, deep-rooted trees passively transfer water at night from deep moist soil to shallow dry soil, or from moist shallow to dry deep soil layers, a phenomenon called ‘hydraulic redistribution’ (Oliveira *et al.*, 2005). If many tropical forests exhibit this redistribution behaviour, the effects of increased evaporative demand with warming may be buffered for shallow-rooted species.

Variation in xylem architecture may also affect species’ ability to adapt to warmer temperatures. Lianas (woody vines) can transpire more water than trees of the same diameter, but are more susceptible to drought-induced embolisms (Fisher & Ewers, 1995). In the Neotropics, lianas have increased in abundance over the last two decades, possibly as a result of increasing atmospheric CO₂ (Phillips *et al.*, 2002; Schnitzer & Bongers, 2011), which could mean that forests as a whole may become more susceptible to greater water stress with the increasing dominance of lianas. On the other hand, high liana cover has been found to buffer host tree sap flow responses to climatic extremes in a Costa Rican rain forest (O’Brien *et al.*, 2004). The diversity of root architecture, soil water partitioning, and hydraulic architecture are not well explored in tropical forests, and would be important baseline data for our understanding of how water balance may be affected by the increased evaporative demand that would come hand-in-hand with increased temperatures.

(4) Photosynthesis and stomatal conductance

Photosynthesis increases with increasing measurement temperature (temperature of air, soil, or plant material measured at the time of sampling) up to a thermal optimum, then decreases (Berry & Bjorkman, 1980). Thermal optima greatly depend upon genetic factors and growth temperatures (temperature at which plants/microbes are grown or incubated), with tropical tree species showing sharp declines in leaf-level photosynthesis between measurement temperatures of 33 and 40 °C (Fig. 2; Koch, Amthor & Goulden, 1994; Lerdau & Keller, 1997; Doughty & Goulden, 2008; Doughty, 2011). Midday depression of photosynthesis has been measured in tropical forest tree canopies at the leaf-level (Koch *et al.*, 1994), coinciding with the hottest part of the day and the highest leaf-to-air VPD. The direct cause of this midday depression of net photosynthesis is often difficult to determine because the effects of elevated temperature on photosynthesis can be broken down into two primary driving mechanisms: mesophyll (direct) and stomatal (indirect) effects (Lloyd & Farquhar, 2008).

Many biochemical processes in the mesophyll are directly affected by increasing temperature (Sage & Kubien, 2007). Under historical atmospheric CO₂ concentrations (<380 ppm) and above a thermal optimum for plants (>35 °C), the primary limiting factor for photosynthesis is a reduction in Rubisco’s carboxylation activity (Farquhar, Von Caemmerer & Berry, 1980). Under current and future CO₂ concentrations (>380 ppm), however, the primary limitations on C3 photosynthesis above a thermal optimum are electron transport rate and Rubisco activase function

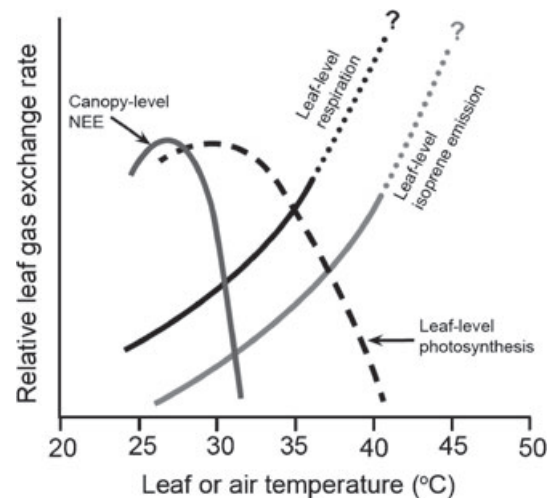


Fig. 2. Relative canopy gas exchange rates of tropical trees in response to increasing leaf temperature (for leaf-level photosynthesis, respiration, and isoprene emission) or increasing air temperature (for net ecosystem exchange, NEE). Relationships are based on tropical tree temperature thresholds for leaf-level photosynthesis (Koch *et al.*, 1994; Lerdau & Keller, 1997; Doughty & Goulden, 2008), temperature thresholds for canopy-level net ecosystem exchange (Doughty & Goulden, 2008), leaf-level foliar respiratory Q_{10} values (Meir *et al.*, 2001; Cavaleri *et al.*, 2008), and leaf-level foliar isoprene emission rates (Lerdau & Keller, 1997) found in the literature. Leaf-level rates represent short-term responses (minutes), while the canopy-level rate represents data from a longer term study (1 year). Dotted lines represent extrapolations beyond the data.

(Sage & Kubien, 2007). Electron transport rates of tropical species decline between approximately 35 and 40 °C, but this process is largely reversible (Sage & Kubien, 2007; Lloyd & Farquhar, 2008). The irreversible denaturation of Rubisco activase (a key enzyme that regulates the function of Rubisco) may be a primary cause of photosynthesis limitation above approximately 42 °C (Sage & Kubien, 2007). The biochemical acclimation potential of photosynthesis under warmer growth temperatures has been associated with either an increase in heat stability of Rubisco activase or an increased capacity for electron transport (Berry & Bjorkman, 1980; Sage & Kubien, 2007). Biochemical acclimation is a specific form of thermal acclimation whereby plants or microbes equilibrate to new measurement temperatures *via* biochemical adjustments such as enzyme or membrane stabilization. We define thermal acclimation as the adjustment of the rate of a plant or microbial process in response to a new growth temperature. Mechanisms may include: biochemical acclimation, substrate limitation, and/or a change in microbial community structure.

As temperature increases, so too does VPD, which indirectly decreases the rate of photosynthesis by inducing stomatal closure to avoid water stress (Lloyd & Farquhar, 2008). Teasing apart mesophyll *versus* stomatal effects can be challenging (Lewis, Malhi & Phillips, 2004; Doughty & Goulden, 2008). A simple leaf model using known temperature

sensitivities of tropical species showed reductions in photosynthesis above thermal optima to be almost entirely due to indirect stomatal responses (30%), as opposed to direct biochemical effects on photosynthetic machinery (2%) (Lloyd & Farquhar, 2008). On the other hand, a recent canopy leaf warming experiment in the Amazon found reductions in photosynthetic capacity to be primarily the result of irreversible damage to photosynthetic machinery, rather than CO₂ limitation due to stomatal closure (Doughty, 2011).

Leaf-level gas-exchange studies in Australia have shown that tropical species have lower photosynthetic thermal acclimation potential than temperate species, suggesting that tropical species may be more susceptible to climate change because they develop under lower seasonal and day-to-day temperature variation (Cunningham & Read, 2003b). This theory is further supported by *in situ* leaf warming experiments in the Amazon showing no evidence of photosynthetic thermal acclimation in response to 13 weeks of 2–5 °C warming of existing leaves (Doughty, 2011). Given the recent evidence, tropical plants appear to be unable to thermally acclimate their photosynthetic machinery, suggesting a decrease in overall forest C sink potential with global warming. It is unclear, however, whether or not plants will be able to thermally acclimate under naturally warming conditions, which occur more slowly than experimental warming conditions.

The eddy covariance datasets mentioned previously found that temperature thresholds of canopy-level photosynthesis were substantially lower (approximately 27 °C) than temperature thresholds of leaf-level photosynthesis (approximately 33 °C, Fig. 2), suggesting an important disconnect between leaf-level and whole-canopy level C assimilation sensitivities to temperature. Highlighting this phenomenon, a recent study in Amazonia found approximately 10 °C difference in the temperature thresholds of leaf-level *versus* canopy-level photosynthesis (Doughty & Goulden, 2008). The disconnect was attributed to vertical heterogeneity of warming within the canopy, where sunlit leaves can warm to well above bulk canopy air temperature, while shaded leaves remain relatively cool (Doughty & Goulden, 2008). The warmed, well-lit leaves can exceed leaf temperature thresholds for photosynthesis, causing overall decreases in C gain. Because these upper leaves contribute disproportionately more to whole-canopy C flux, the net effect is a reduction in canopy CO₂ exchange even when the bulk air temperature is well below leaf temperature thresholds for photosynthesis (Fig. 2; Doughty & Goulden, 2008).

Doughty & Goulden (2008) argue that their results support the theory that Amazonian tropical forests are currently near a high-temperature threshold. Further evidence of this theory is found in palaeoclimate and palaeoecological studies which find that the Amazon is presently experiencing climate outside its historic range of variability (Maslin *et al.*, 2005), and even moderate warming has the potential to push the system beyond a critical threshold and induce positive warming feedbacks (Cowling *et al.*, 2004). However, Lloyd & Farquhar (2008) dispute this theory using a leaf-level model

of photosynthesis to show that tropical forests are in fact well below their temperature threshold. These interpretations may not be mutually exclusive, however, because Lloyd & Farquhar (2008) modeled leaf-level photosynthesis and leaf temperature, not canopy-level photosynthesis and air temperature. If Doughty & Goulden (2008) are correct in their assessment of leaf *versus* canopy disconnects, then bulk air temperature may in fact be well below the leaf-level photosynthesis temperature threshold and still have a negative effect on C assimilation for the entire canopy (Fig. 2).

(5) Respiration

Foliar respiration increases exponentially with measurement temperature in the short term (minutes to hours), with overall mean foliar Q₁₀ values ranging from 1.8 to 2.3 for tropical forest trees (Fig. 2; Meir, Grace & Miranda, 2001; Cavaleri, Oberbauer & Ryan, 2008). However, these short-term responses may not be applicable to predicting long-term temperature responses (days to years), because respiratory thermal acclimation may be primarily driven by substrate supply, which is controlled by net photosynthesis (Saxe *et al.*, 2001). In a cross-biome analysis, Saxe *et al.* (2001) found that the long-term effects of temperature are ultimately driven by the thermal acclimation of photosynthesis rather than respiration. However, a recent meta-analysis across global functional types and biomes showed that leaf-level measurements of photosynthesis did not acclimate to temperature, while leaf-level respiration did (Way & Oren, 2010). This study, together with the limited ability of tropical photosynthesis to acclimate thermally (Cunningham & Read, 2003b; Doughty, 2011), suggests that tropical species may not be able to maintain positive C balance under warmer conditions. To date, there have been no investigations of the long-term effects of warming on tropical tree respiration.

(6) Biogenic volatile organic compound emission

Biogenic volatile organic compounds (BVOCs), especially isoprene, have been found to diffuse from stomata of 30–50% of tested tropical tree species throughout the world (Lerdau & Keller, 1997; Harley *et al.*, 2004). Tropical forest isoprene emission is the most important individual source of photochemically reactive compounds in the atmosphere globally, and isoprene emissions increase exponentially with increasing measurement temperatures at the leaf level in the short term (minutes to hours) (Fig. 2; Lerdau & Keller, 1997). Above approximately 38 °C, isoprene emission from tropical forests may be a significant source of assimilated C lost to the atmosphere (Clark, 2004; Harley *et al.*, 2004). One of the primary functions of foliar isoprene is to increase thermo-tolerance of photosynthetic machinery (Sharkey, Wiberley & Donohue, 2008); however, isoprene may not help plants tolerate long-term sustained warming (days to years) (Sharkey *et al.*, 2008). Like foliar respiration, thermal acclimation potential of BVOC emission is likely directly linked to net photosynthetic uptake over the long term, although this has not been investigated in tropical forests.

(7) Synthesis: above-ground processes and drivers

The apparent effects of warming on above-ground tropical forest tree physiology differ depending upon the spatial and temporal scale of investigation. At the stand level, the diversity of both growth response and suggested climatic drivers may indicate that there is no single response of tropical forests to increasing temperatures, and conclusions vary among locations due to differing measurement techniques. If above- *versus* below-ground C allocation, whole-tree morphology, and source-sink feedbacks can be affected by warming, then the standard diameter at breast height (DBH)-based forest inventory methods may not be sufficient to detect effects of changing temperatures. A more holistic approach to stand-level measurements may be warranted, including a combination of DBH and height measurements with more ecophysiological mass-balance approaches of measuring C allocation, both above and below ground.

A better understanding of both leaf-level and canopy-level responses to warming also warrants a multi-scale approach. The disconnects between stomatal and whole-canopy conductance, and between leaf- and canopy-level photosynthesis, indicate that experiments which combine the two approaches can yield emergent patterns that may not be seen with either approach alone. Photosynthetic temperature thresholds, for example, should be investigated both in controlled chamber experiments and whole-canopy flux experiments. When investigating canopy-scale fluxes, temporal scale becomes important as well. For example, more and more long-term eddy flux studies (3+ years) are revealing inter-annual patterns that were not detected by shorter term investigations. A multi-scale approach will be crucial for the success of modeling efforts.

While it is important to understand individual drivers of climate change (e.g. warming), often it is impossible to tease apart the effects of increased temperature from the effects of water stress. The diversity of root architecture, soil water partitioning, and hydraulic architecture are not well explored in tropical forests, and would be important baseline data for our understanding of how water balance may be affected by the increased evaporative demand that would come hand-in-hand with increased temperatures. At the leaf level, experiments investigating the relative importance of both stomatal closure due to water stress and direct temperature effects on mesophyll processes will help us gain a better understanding of the relative importance of warming *versus* water stress on canopies, especially with respect to thermal acclimation potential of photosynthesis, which likely controls long-term thermal acclimation of both respiration and isoprene emission (Fig. 1).

IV. BELOW GROUND

(1) Litter and root production

Temperature-induced changes in forest productivity, below-ground C allocation, and stress-induced leaf drop could

all contribute to increased inputs of C into soils. While cross-site comparisons suggest a significant positive effect of increased temperature on below-ground C allocation and litterfall production (Silver, 1998; Raich *et al.*, 2006), we found no conclusive data within individual tropical forest sites to support a strong positive effect of temperature on soil C inputs, with the exception of a 7-year study of root dynamics that shows a relatively weak correlation between MAT and dead root biomass in a wet tropical forest in Costa Rica (Espeleta & Clark, 2007). Given the low variability in temperature in tropical ecosystems, longer time series (10+ years) are likely needed to reveal relationships between litterfall, root production and temperature in tropical forests (Clark & Clark, 2011), nevertheless, these datasets are rare.

In turn, an increase in fresh litter inputs and deep rooting could also stimulate additional CO₂ loss from soils (Kuzyakov, 2010). In seasonal forests in Brazil, both the mass and distribution of litter and roots have been shown to explain a large degree of the spatial variability in soil respiration (Sotta *et al.*, 2006; Metcalfe *et al.*, 2007). In addition, a twofold litter addition experiment in a seasonal forest in Panama significantly increased soil respiration rates, which suggests a priming of recalcitrant C decomposition in response to the additional fresh litter inputs (Sayer, Powers & Tanner, 2007). Despite the potential for priming to significantly affect C storage and fluxes in tropical soils, the importance of this mechanism for the overall C budget remains uncertain (Subke, Inglima & Cotrufo, 2006; Kuzyakov, 2010). The high spatial and temporal variability in litter and root inputs at the small scale (e.g. millimeters) could create 'hot spots' of elevated soil respiration that are difficult to measure at large scales (e.g. hectares) (Kuzyakov, 2010). Variability in litter inputs could additionally affect the rate of C stabilization due to indirect effects of litter on the soil environment, influencing factors such as soil pH, soil moisture, soil organic matter (SOM) chemistry and nutrient availability (Sayer, 2006; but see Wood & Lawrence, 2008). Overall, increased C inputs may affect a range of ecological processes related to C cycling and storage, and resolving how litter and root production will respond to elevated temperatures is necessary to predict accurately the effects of warming on C dynamics in tropical forests.

(2) Heterotrophic soil respiration

Kinetic theory states that reaction rates increase with increasing temperature up to a thermal optimum, at which point either microbial function or substrate availability become limiting, and reaction rates decline (Fig. 3A; Davidson & Janssens, 2006). We might therefore expect temperature to limit decomposition rates in cooler climates and C availability and/or the surpassing of microbial thermal optima to limit decomposition in warmer climates (Fig. 3A; Davidson & Janssens, 2006). There are currently no published *in situ* soil-warming experiments in the tropics; however, experimental warming in temperate and high-latitude ecosystems find that soil respiration initially increases in response to

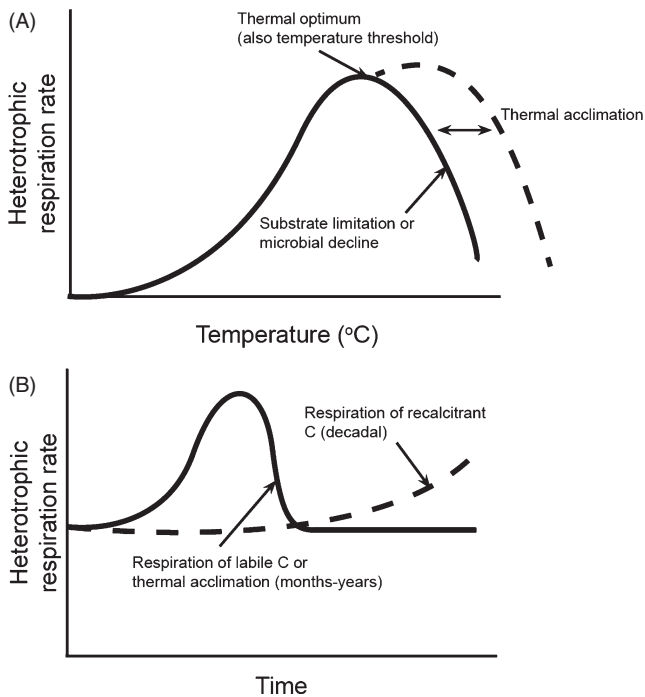


Fig. 3. (A) Kinetic theory suggests that heterotrophic respiration rates will increase with temperature up to a thermal optimum, at which point either microbial function declines or substrate limitation occurs. Thermal acclimation of the microbial community can increase the temperature optimum (i.e. high temperature threshold). (B) Thermal acclimation of heterotrophic respiration could occur as a result of substrate limitation, a shift in microbial community, or biochemical acclimation to increased temperature in the short term (months to years). High sensitivity of recalcitrant C to increased temperature could lead to significant soil C loss in the long term (decadal).

soil warming, but typically returns to control values within a few years of treatment (Fig. 3B; Oechel *et al.*, 2000; Luo *et al.*, 2001; Kirschbaum, 2004). Various theories have been put forth to explain this observed thermal acclimation of soil respiration (Kirschbaum, 2000; Davidson & Janssens, 2006; Bradford *et al.*, 2008; Kleber, 2010), yet how these theories apply to tropical forested ecosystems remains highly uncertain. Soil incubation experiments suggest that tropical microbes have thermal optima higher than their cooler climate counterparts (Balser & Wixon, 2009), and temperature thresholds are not readily observed in short-term incubations (Holland *et al.*, 2000). In particular, laboratory experiments using tropical soils have revealed elevated soil respiration rates at growth temperatures as high as 55 °C, well beyond the predicted temperature increases for tropical regions (Holland *et al.*, 2000; Balser & Wixon, 2009). These data suggest it is unlikely that increased temperature will push microbial respiration past its biochemical thermal optimum, and the size and composition of the soil C pool (i.e. substrate availability) may be more likely to constrain the temperature sensitivity of decomposition in tropical forests.

There is large disagreement as to which C pool characteristics control the temperature sensitivity of soil C decomposition (Davidson & Janssens, 2006; Kirschbaum, 2006; von Lütow & Kogel-Knabner, 2009). One hypothesis is that soil C loss will be constrained by the size of the labile C pool, and that once this pool is depleted respiration rates will slow and ultimately be maintained by new soil C inputs (Fig. 3B; Giardina & Ryan, 2000). Others argue that, because recalcitrant C is more sensitive to increased temperature than labile C, we could expect a more substantial temperature-induced loss of soil C in the long term (decades) than previously predicted (Fig. 3B; Davidson & Janssens, 2006; Conant *et al.*, 2008). There is also evidence that labile and recalcitrant C do not differ in their sensitivity to temperature (Fang *et al.*, 2005). Taken together, tropical soil incubation experiments suggest that soil C loss will increase with temperature (Holland *et al.*, 2000; Knorr *et al.*, 2005); however, the magnitude and scale (spatial and temporal) of this loss remains unknown. Given that tropical forests store more soil C than any other terrestrial biome—containing 40% more soil C than temperate and boreal forests combined (Jobbagy & Jackson, 2000)—any increase in decomposition rates in these systems is likely to affect the global C balance.

In addition to substrate limitation, soil respiration could be affected by changes in the composition and/or overall function of the microbial community (i.e. thermal acclimation; Bradford *et al.*, 2008; Balser & Wixon, 2009). A cross-site comparison of three forests (taiga, temperate and tropical) found that despite similar microbial biomass, taiga respiration rates were significantly lower than tropical forest rates when soils were incubated at the same temperature, suggesting inherent differences in basal metabolic activity of the microbial communities (Balser & Wixon, 2009). Additionally, microbes may respond to increased temperature by altering C allocation (Allison, Wallenstein & Bradford, 2010). Microbes release enzymes that break down SOM. The acquired resources can then be used to produce more enzymes, increase microbial biomass, and/or to maintain microbial activity (Allison *et al.*, 2010). Shifting C allocation among these pathways can affect the fate of soil C and the rate of microbial respiration, consequently determining the loss of C from soil (Allison *et al.*, 2010). Due to the amount of C cycled by soil microbes, a change in microbial C use efficiency (the proportion of microbially processed C respired as CO₂ versus the proportion allocated to microbial biomass) could have significant effects on C stored and lost from tropical forests. Finally, microbes could acclimate biochemically to increased temperature (e.g. produce enzymes with higher temperature thresholds), thereby showing an initial temperature-induced increase in respiration, followed by a rapid return to initial rates (Fig. 3B; Bradford *et al.*, 2008). If soil microbial biochemical acclimation proves common across tropical ecosystems, it could significantly reduce the potential stimulatory effect of increased temperature on decomposition rates. At this time however, the response of tropical forest microbial community composition and

function to increased temperature remains untested outside of the laboratory.

(3) Abiotic effects of temperature on SOC

In addition to biotic controls on soil organic C (SOC), temperature could also affect abiotic processes related to C availability in a variety of ways. Higher temperatures could decrease the sorption of SOC to the mineral surface, resulting in an increase in C availability (von Lützow *et al.*, 2006). Conversely, higher temperatures may also increase SOC protection from decomposition, which would reduce C availability (Thornley & Cannell, 2001). Temperature may further influence C dynamics by increasing the diffusion of C substrates into the soil-water phase. This increased diffusion could increase microbial access to SOC and thereby increase microbial decomposition (Davidson, Janssens & Luo, 2006). However, soils also tend to become drier as temperature increases, and lower soil water content could restrict microbial access to these compounds and thus increased temperature could also reduce microbial decomposition *via* indirect effects of temperature on soil water availability (Grant & Rochette, 1994; Davidson *et al.*, 2006). Finally, increased temperature may also influence soil pH (e.g. increasing concentrations of dissolved gases in soil pore water which alters the pH). Soil pH is known to influence enzyme activation energies and soil microbial community composition, and consequently SOC decomposition rates (Kleber, 2010). Currently, little is known about temperature effects on these processes in tropical forests, nor their potential to affect SOC decomposition in a warmer world (Davidson & Janssens, 2006).

(4) Autotrophic soil respiration

Root respiration (autotrophic respiration) is estimated to account for 24–38% of total soil respiration in some tropical forests (Silver *et al.*, 2005; Sayer & Tanner, 2010), and litter and root biomass can explain as much as 44% of observed spatial variability in tropical forest soil respiration rates (Metcalfe *et al.*, 2007). Moreover, differences in the relative time scale and response magnitude of autotrophic *versus* heterotrophic components could affect interpretations of total soil respiration responses to temperature (Subke & Bahn, 2010).

Findings from temperate forests suggest that root respiration is more sensitive to temperature than heterotrophic respiration (Epron *et al.*, 2001). However, more recent research suggests that differences in root respiration may be driven largely by variability in substrate supply from photosynthesis (Ruehr & Buchmann, 2010). This rapid link between canopy and soil processes is illustrated by the rapid recovery of $^{13}\text{CO}_2$ and $^{14}\text{CO}_2$ in the soil CO_2 efflux within days of canopy labeling in temperate forests, as well as a 37% decline in soil respiration within days of tree girdling in a boreal forest (Högberg & Read, 2006). Given evidence of strong ties between root respiration and photosynthesis, root respiration will likely acclimate to longer term warming as

a result of substrate limitation if warming causes decreased overall photosynthesis rates.

Spatial variation in root abundances can also influence our interpretation of temperature effects on soil respiration. In a wet tropical forest in Costa Rica, Schwendenmann *et al.* (2003) found a strong positive relationship between temperature and CO_2 concentration in the deeper soils (e.g. below the rooting zone), while both soil moisture and temperature were important controlling factors of soil respiration in the top 1 m (where the majority of roots are concentrated). Davidson *et al.* (2000) found a strong trend of increasing CO_2 efflux with temperature in a tropical pasture in Brazil; however, the diurnal fluctuations of soil respiration were greater than seasonal variation, suggesting the temperature response was actually driven by diurnal changes in photosynthate allocation to roots rather than a direct response to temperature. Despite its importance to our overall understanding of total soil respiration, there are currently no studies we know of that directly investigate the thermal acclimation potential of root respiration in tropical forests. Differences in the relative time scale and magnitude of the responses of autotrophic *versus* heterotrophic components, and investigations into biochemical acclimation and substrate limitation could strongly affect interpretations of total soil respiration responses to temperature (Subke & Bahn, 2010).

(5) Synthesis: controls on below-ground C storage

Whether or not warming will have a positive effect on soil C inputs is vital to determining the net effect of temperature on soil C storage. While multiple cross-site comparisons suggest temperature will lead to an increase in C inputs, we found little evidence within tropical forest sites to support this result. Much longer time series (10+ years) are likely needed to reveal these relationships; however, these data sets do not currently exist for tropical forests. Our ability to predict temperature effects on C inputs will therefore depend heavily on our ability to resolve temperature sensitivities of above-ground processes (e.g. C allocation in plants).

Studies that directly investigate the temperature sensitivity of soil C loss from tropical forests are notably rare. As such, the majority of our predictions regarding the temperature sensitivity of soil C decomposition are primarily theoretical. Nevertheless, the general consensus is that increased temperature will result in additional C respiratory losses from tropical soils. There is considerable uncertainty however as to the magnitude and time scale of this loss. While additional laboratory experiments will be useful for evaluating the temperature sensitivity of specific mechanisms, they are short in duration (≤ 1 year), involve significant disturbance of the soil matrix, exclude autotrophic responses, and cannot account for the effect of altered C inputs. The effects of warming on below-ground processes are likely to be varied in both time and space (Rustad *et al.*, 2001). We therefore see great benefit in the establishment of long-term (10+ years), field-based temperature manipulation experiments in tropical forests. Given evidence of a strong link between above- and below-ground processes, these

experiments could greatly benefit from incorporating the whole-system response to warming (Fig. 1). However, due to the challenges of scaling a warming manipulation to the forest level, mesocosm experiments that include both plant and soil warming could provide a more immediate way forward.

V. INDIRECT CONTROLS ON C BALANCE

(1) Litterfall quality

Litterfall is the major pathway for transferring C and nutrients to the soil. It follows that changes in litter quality could significantly affect a suite of processes associated with C cycling and storage in tropical forests (Vitousek, 1984). For example, increased inputs of low-quality litter (e.g. high lignin:N ratios) could reduce decomposition rates, resulting in a greater proportion of litterfall C being stabilized within the forest floor. By contrast, increased litter quality (e.g. lower lignin:N ratios) could lead to greater microbial respiration and loss of C as CO₂ (Vitousek, 1984). These changes in litter quality could also feed back to affect future forest productivity, resulting in more C stored in plant biomass (Wood *et al.*, 2009). Analyses of total fine litterfall across five tropical forest elevation gradients showed a strong positive relationship between litter N and temperature (Silver, 1998). By contrast, a 7-year study in secondary forest in Costa Rica found total fine litter N to decline in response to small increases in minimum temperature (Tully & Lawrence, 2010), suggesting the possibility of a negative effect of temperature on foliar (i.e. live leaf) N. Studies in other ecosystems (temperate forest, grassland, tundra) have found both positive and negative effects of temperature on foliar N concentrations (Arft *et al.*, 1999; Hobbie *et al.*, 2001; An *et al.*, 2005). Overall, studies that report temperature effects on litterfall quality in tropical forests are rare, and we found none that reported effects on nutrients other than N (e.g. P or Ca).

(2) Soil nutrient availability

Temperature-induced changes to soil nutrient availability could indirectly affect the C balance of tropical forests (Hungate *et al.*, 2003). Soil nutrient availability has been shown to affect forest productivity and foliar nutrient concentrations, as well as rates of net photosynthesis and dark respiration (Meir *et al.*, 2001). Wardle *et al.* (2005) suggested that the availability of nutrients strongly limits productivity in highly weathered soils, such as those found in many tropical forests, and that forests on such soils have the potential to be more productive if their soils were more nutrient rich. McKane *et al.* (1995) also suggested that C:nutrient interactions will constrain increases in C storage, resulting in a maximum increase of 16% above present-day stocks within the next 200 years. Nutrient availability also affects the rate of soil C loss *via* effects on soil

respiration and decomposition rates (Cleveland & Townsend, 2006). Accordingly, temperature-nutrient interactions have the potential to affect C cycling in tropical forest soils. A long-term N fertilization study in Puerto Rico found that recalcitrant C in N-fertilized soils had much longer turnover times than in unfertilized soils; however, under elevated temperatures the N-fertilized soils lost significantly more recalcitrant C than unfertilized soils (Cusack *et al.*, 2010). Taken together, these results suggest that C efflux and long-term stability of C stocks in tropical soils depend upon nutrient availability and temperature as well as their interaction.

Temperature may affect multiple aspects of N and P cycling in the tropics, including N fixation, nitrification, denitrification (Sierra, 2002; Houlton *et al.*, 2008), and phosphatase activity (Gholz *et al.*, 2000; Sierra, 2002). While there are no published field warming experiments in the tropics, evidence from soil-warming experiments in temperate and high-latitude ecosystems have found large increases (46%) in N mineralization rates in response to warming (Rustad *et al.*, 2001). By contrast, laboratory results synthesized by Houlton *et al.* (2008) suggested that N inputs from N fixation may decline at temperatures above 26 °C. If this response holds under field conditions, increased temperatures in many tropical forests could result in decreased N inputs. Increased temperatures could also affect the relative proportions of different forms of soil N (e.g. NO₃⁻ versus NH₄⁺). For example, if nitrification rates increase relative to other N cycling pathways, soils may maintain higher NO₃⁻:NH₄⁺ ratios. Variation in the proportion of different soil N pools has been shown to affect a variety of ecosystem characteristics, such as decomposition rates, plant cover and, ultimately, C cycling (Austin, Sala & Jackson, 2006). Warmer temperatures could also stimulate additional N losses (in particular NO₃⁻) *via* increased denitrification rates. As a set of enzymatic processes, denitrification is sensitive to changes in temperature; however, this and many N cycling responses are likely to vary by soil type (Stanford *et al.*, 1975). Overall, there are a suite of mechanisms through which temperature increases could affect soil N cycling, N pools and the relative proportions of different N molecules.

Increased temperature is also likely to affect P availability, which could be especially important for tropical forests given the likelihood of P limitation in these systems (Vitousek, 1984; Vitousek & Farrington, 1997; Cleveland, Reed & Townsend, 2006; McGroddy & Silver, 2011). Laboratory studies suggest that increased temperature can increase phosphatase activity, which could in turn increase P availability and thus stimulate plant growth and/or soil respiration (Vitousek & Farrington, 1997; Cleveland & Townsend, 2006). Increased temperature could further increase P availability by reducing the sorption of phosphate (Barrow, 1984). However, if the binding of inorganic and organic P to soil decreases in response to high temperature, loss of P to leaching could also increase (Hedin, Vitousek & Matson, 2003). Overall, despite the potential for strong regulatory effects, our understanding of the potential response of nutrient availability to increased temperature is

not well understood for tropical forests. Accordingly, our limited perspective hinders predictions of how temperature may affect tropical forest C cycling indirectly *via* effects on nutrient cycles.

(3) Temperature interactions with water, CO₂ and light

Temperature is likely to interact with other environmental variables such as water availability, atmospheric CO₂ and solar radiation levels. While a full exploration of these interactions is beyond the scope of this review, we briefly mention here the primary uncertainties in the literature surrounding temperature interactions with other abiotic factors.

There is currently large uncertainty as to how precipitation patterns will change in tropical regions, with some regions expecting more precipitation, some less, and some a change in timing (Christensen *et al.*, 2007). In addition to the effects of temperature on the water use of trees (Section III.3) and the indirect effects of low air humidity on photosynthesis *via* stomatal closure (Section III.4), temperature is also likely to affect soil moisture directly through changes to evaporation and relative humidity. A change in soil moisture has many varied and cascading effects on soil processes including, but not limited to, soil respiration (Vasconcelos *et al.*, 2004; Davidson *et al.*, 2008), decomposition (Meentemeyer, 1978; Wieder, Cleveland & Townsend, 2009), soil redox reactions (Silver, Lugo & Keller, 1999; Chacon *et al.*, 2006), microbial activity (Kieft, Soroker & Firestone, 1987; Grant & Rochette, 1994; Cleveland *et al.*, 2004), and nutrient availability (Lodge, McDowell & McSwiney, 1994; McGrath, Comerford & Duryea, 2000). Separating the effects of temperature from those of moisture availability in natural settings represents a significant challenge.

While there is currently no CO₂-addition experiment in any tropical forest, results from studies in temperate forests show CO₂ fertilization effects in response to elevated atmospheric CO₂ levels, including higher C production, greater water-use efficiency, and lower stomatal conductance (Ainsworth & Long, 2005). While some researchers suggest this CO₂ fertilization effect is also occurring in tropical forests, whether or not tropical forests have experienced increased growth with elevated atmospheric CO₂ levels remains controversial (Lloyd & Farquhar, 2008; Lewis *et al.*, 2009a). Nevertheless, if increased CO₂ does result in increased growth and water-use efficiency, the negative effects of increased temperature (and possible changes to rainfall regimes) would likely be reduced.

Finally, the amount of incoming solar radiation can significantly affect biological processes related to C cycling, most notably, photosynthesis. There is evidence that solar radiation varies on decadal time scales (Wild, 2009) and researchers have found evidence that an increase in anthropogenic aerosols in the atmosphere may result in global dimming (Rotstayn & Lohmann, 2002; Wielicki *et al.*, 2002; Lewis *et al.*, 2004; Wild, 2009). If light is indeed decreasing as temperature increases, we may expect reduced

C uptake by plants due to lower photosynthetic rates (from lower light) and additional C loss from soils in response to increased temperature. Taken together, these concurrent changes could significantly reduce any net tropical forest C sink. However, given that light and temperature often co-vary on seasonal time scales, teasing apart their individual effects on ecosystem processes represents a significant research challenge. Experimental warming could help refine our understanding of the differential effects of these key drivers of ecosystem processes.

(4) Synthesis: indirect controls on C cycling

Current modeling efforts highlight the large role nutrient cycling could play in the response of net C flux to climate change (e.g. Wang & Houlton, 2009), and the few tropical fertilization studies that exist support this conclusion. In fact, temperature effects on nutrient cycling and availability could have a stronger influence on tropical C cycling than the direct effect of temperature change; however, the magnitude and extent of such changes remain unknown. The complexity of these interacting controls (i.e. temperature and nutrient availability) further confounds our ability to forecast future C cycling. Explicit studies in field settings would greatly facilitate accurate predictions of how temperature will affect C, N and P cycles that are tightly coupled in the real world. That said, laboratory and greenhouse studies could elucidate specific mechanisms behind temperature effects on nutrient availability so that we can begin to parcel out the likelihood and extent of these potential controls. The effects of increased temperature on N and P cycles when natural microbial communities, plant responses (e.g. C allocation), and other such complicating factors are included remain wholly unknown (Fig. 1).

Global warming is likely to be accompanied by other environmental changes (e.g. rising atmospheric CO₂ concentrations), and these changes will interact with temperature in complex ways. However, while multi-factor experiments are valuable for testing concepts, these experiments can be difficult to design, conduct, and interpret. Single-factor experiments that focus on increasing our understanding of mechanisms may provide a reasonable way forward and a complement to both modeling and future large-scale endeavours (Norby & Luo, 2004).

VI. CONCLUSIONS

(1) Over the last decade, debates regarding the primary forces driving changes in tropical forest C balance have been vigorous (e.g. Wright, 2005). Even with the full weight of the current evidence, an all-encompassing theory about what is happening and what will happen to tropical forests with global warming remains elusive.

(2) We suggest three main reasons for this. First, there is a general lack of data at and across the appropriate scales. While there is evidence to suggest that temperature

will significantly affect important processes related to C cycling and storage in tropical forests, we found insufficient support in the literature to conclude with any certainty what the direction of this response is likely to be. Second, research conducted at different spatial and temporal scales often leads to contradicting conclusions. Large-scale observational studies confound multiple climatic, edaphic, and biotic factors, while small-scale studies cannot address the interconnectedness of above- and below-ground processes and are challenging to scale to the ecosystem. Third, tropical forests vary enormously in factors such as soil type and community composition (Townsend, Asner & Cleveland, 2008), which are known to influence ecosystem function. Thus, the likelihood that all tropical forests will respond similarly is low.

(3) We propose the following recommendations for future research that may help resolve some of the current uncertainties: (i) the majority of tropical forests already experience temperatures $>20^{\circ}\text{C}$. As such, our ability to use temperature gradients within the tropics to predict accurately their response to increased temperature is limited. There is currently no large-scale field-warming manipulation anywhere in the tropics, and we submit there is a dire need to attempt this in order to tease apart effects of temperature *versus* those of other environmental variables. (ii) The assortment of trajectories in tropical forests may be as diverse as the forests themselves, and the primary drivers of change may depend on multiple limiting factors. It is therefore important that we incorporate a range of tropical forest sites into our experiments and models. Ideally this would involve a network of tropical forest sites with coordinated efforts to ensure that methodological differences do not hinder comparisons [e.g. Center for Tropical Forest Science (CTFS), Amazon Forest Inventory Network (RAINFOR)]. (iii) Evidence suggests a tight interconnectedness between above- and below-ground processes (e.g. photosynthesis and root respiration). Warming may also affect C allocation patterns (e.g. tree morphology, C allocation of microbes) that could be missed by focusing on above- or below-ground components alone. Large-scale forest warming experiments would ideally be established to address these uncertainties. However, mesocosm experiments that include both plant and soil warming could accomplish some of the same goals. (iv) Long-term experiments are crucial (Luo *et al.*, 2011). The recalcitrant C pool is likely to respond to environmental change on decadal time scales. Thermal acclimation of photosynthesis and/or microbial processes are also likely to occur over time scales longer than a season. As such, short-term manipulations (≤ 1 year) are unlikely to capture these critical responses. (v) There currently exists a large disconnect between findings obtained at different spatial scales. For example, temperature thresholds of photosynthesis depend on whether one is looking at the leaf-level (leaf temperature) or the canopy level (air temperature). Similarly, warming may differentially affect heterotrophic *versus* autotrophic soil respiration. Incorporating a range of scales into experiments will greatly improve our ability to

understand mechanistically what is happening to tropical forests under warming conditions (see Fig. 1). (vi) Finally, there are some areas of tropical forest research where almost no field data on temperature response are available, including nutrient cycling, heterotrophic *versus* autotrophic respiration, thermal acclimation *versus* substrate limitation of plant and microbial communities, below-ground C allocation, temperature effects on species composition (plant and microbial), hydraulic architecture of roots, and the sensitivity of soil C loss to temperature.

(4) Whether or not tropical forests will become a source or a sink of C in a warmer world remains highly uncertain. Given the importance of these ecosystems to the global C budget, resolving this uncertainty remains a critical research priority.

VII. ACKNOWLEDGMENTS

We gratefully acknowledge M.G. Ryan, S.J. Van Bloem, A.E. Lugo, and two anonymous reviewers for their insightful comments and edits on earlier drafts of this manuscript. Support for this research was provided by the USDA Forest Service International Institute of Tropical Forestry.

VIII. REFERENCES

- AINSWORTH, E. A. & LONG, S. P. (2005). What have we learned from 15 years of free-air CO_2 enrichment? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytologist* **165**, 351–371.
- ALLISON, S. D., WALLENSTEIN, M. D. & BRADFORD, M. A. (2010). Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience* **3**, 336–340.
- AMTHOR, J. S., HANSON, P. J., NORBY, R. J. & WULLSCHLEGER, S. D. (2010). A comment on ‘‘Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality’’ by Aronson and McNulty. *Agricultural and Forest Meteorology* **150**, 497–498.
- AN, Y., WAN, S., ZHOU, X., SUBEDAR, A. A., WALLACE, L. L. & LUO, Y. (2005). Plant nitrogen concentration, use efficiency, and contents in a tallgrass prairie ecosystem under experimental warming. *Global Change Biology* **11**, 1733–1744.
- ANDERSON, B. (2011). Near-term increase in frequency of seasonal temperature extremes prior to the $2\text{--}\infty\text{C}$ global warming target. *Climatic Change* **108**, 581–589.
- ARFT, A. M., WALKER, M. D., GUREVITCH, J., ALATALO, J. M., BRET-HARTE, M. S., DALE, M., DIEMER, M., GUGERLI, F., HENRY, G. H. R., JONES, M. H., HOLLISTER, R. D., JÓNSDÓTTIR, I. S., LAINE, K., LÉVESQUE, E., MARION, G. M., MOLAU, U., MØLGAARD, P., NORDENHÅLL, U., RASZHIVIN, V., ROBINSON, C. H., STARR, G., STENSTRÖM, A., STENSTRÖM, M., TOTLAND, Ö., TURNER, P. L., WALKER, L. J., WEBBER, P. J., WELKER, J. M. & WOOKEY, P. A. (1999). Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs* **69**, 491–511.
- ARONSON, E. L. & McNULTY, S. G. (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology* **149**, 1791–1799.
- AUSTIN, A., SALA, O. & JACKSON, R. (2006). Inhibition of nitrification alters carbon turnover in the Patagonian Steppe. *Ecosystems* **9**, 1257–1265.
- BALSER, T. C. & WIXON, D. L. (2009). Investigating biological control over soil carbon temperature sensitivity. *Global Change Biology* **15**, 2935–2949.
- BARROW, N. J. (1984). Modelling the effects of pH on phosphate sorption by soils. *Journal of Soil Science* **35**, 283–297.
- BERRY, J. & BJORKMAN, O. (1980). Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **31**, 491–543.
- BRADFORD, M. A., DAVIES, C. A., FREY, S. D., MADDOX, T. R., MELILLO, J. M., MOHAN, J. E., REYNOLDS, J. F., TRESIEDER, K. K. & WALLENSTEIN, M. D. (2008). Thermal adaptation of soil microbial respiration to elevated temperature. *Ecology Letters* **11**, 1316–1327.

- BRIENEN, R. J. W., LEBRIJA-TREJOS, E., ZUIDEMA, P. A. & MARTÍNEZ-RAMOS, M. (2010). Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines. *Global Change Biology* **16**, 2001–2012.
- BROWN, S. & LUGO, A. E. (1982). The storage and production of organic-matter in tropical forests and their role in the global carbon-cycle. *Biotropica* **14**, 161–187.
- CAVALERI, M. A., OBERBAUER, S. F. & RYAN, M. G. (2008). Foliar and ecosystem respiration in an old-growth tropical rain forest. *Plant, Cell and Environment* **31**, 473–483.
- CHACON, N., SILVER, W., DUBINSKY, E. & CUSACK, D. (2006). Iron reduction and soil phosphorus solubilization in humid tropical forests soils: the roles of labile carbon pools and an electron shuttle compound. *Biogeochemistry* **78**, 67–84.
- CHAVE, J., CONDIT, R., MULLER-LANDAU, H. C., THOMAS, S. C., ASHTON, P. S., BUNYAVEJCHEWIN, S., CO, L. L., DATTARAJA, H. S., DAVIES, S. J., ESU-FALI, S., EWANGO, C. E. N., FEELEY, K. J., FOSTER, R. B., GUNATILLEKE, N., GUNATILLEKE, S., HALL, P., HART, T. B., HERNANDEZ, C., HUBBELL, S. P., ITOH, A., KIRATIPRAYOON, S., LAFRANKIE, J. V., DE LAO, S. L., MAKANA, J. R., NOOR, M. N. S., KASSIM, A. R., SAMPER, C., SUKUMAR, R., SURESH, H. S., TAN, S., THOMPSON, J., TONGCO, M. D. C., VALENCIA, R., VALLEJO, M., VILLA, G., YAMAKURA, T., ZIMMERMAN, J. K. & LOSOS, E. C. (2008). Assessing evidence for a pervasive alteration in tropical tree communities. *Plos Biology* **6**, 455–462.
- CHRISTENSEN, J. H., HEWITSON, B., BUSUIOC, A., CHEN, A., GAO, X., HELD, I., JONES, R., KOLLI, R. K., KWON, W. T., LAPRISE, R., RUEDA, V. M., MEARN, L., MENÉNDEZ, C. G., RÄISÄNEN, J., RINKE, A., SARR, A. & WHETTON, P. (2007). Regional climate projections. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. SOLOMON, D. QIN, M. MANNING, Z. CHEN, M. MARQUIS, K. B. AVERYT, M. TIGNOR and H. L. MILLER), pp. 848–940. Cambridge University Press, New York.
- CLARK, D. A. (2004). Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* **359**, 477–491.
- CLARK, D. A. & CLARK, D. B. (2011). Assessing tropical forests' climatic sensitivities with long-term data. *Biotropica* **43**, 31–40.
- CLARK, D. A., PIPER, S. C., KEELING, C. D. & CLARK, D. B. (2003). Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences* **100**, 5852–5857.
- CLEVELAND, C. C., REED, S. C. & TOWNSEND, A. R. (2006). Nutrient regulation of organic matter decomposition in a tropical rain forest. *Ecology* **87**, 492–503.
- CLEVELAND, C. C. & TOWNSEND, A. R. (2006). Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 10316–10321.
- CLEVELAND, C. C., TOWNSEND, A. R., CONSTANCE, B. C., LEY, R. E. & SCHMIDT, S. K. (2004). Soil microbial dynamics in costa rica: seasonal and biogeochemical constraints. *Biotropica* **36**, 184–195.
- CONANT, R. T., STEINWEG, J. M., HADDIX, M. L., PAUL, E. A., PLANTE, A. F. & SIX, J. (2008). Experimental warming shows that decomposition temperature sensitivity increases with soil organic matter recalcitrance. *Ecology* **89**, 2384–2391.
- CORLETT, R. T. (2011). Impacts of warming on tropical lowland rainforests. *Trends in Ecology and Evolution* **26**, 606–613.
- COWLING, S. A., BETTS, R. A., COX, P. M., ETTWEIN, V. J., JONES, C. D., MASLIN, M. A. & SPALL, S. A. (2004). Contrasting simulated past and future responses of the Amazonian forest to atmospheric change. *Philosophical Transactions of the Royal Society B: Biological Sciences* **359**, 539–547.
- CRAMER, W., BONDEAU, A., WOODWARD, F. I., PRENTICE, I. C., BETTS, R. A., BROVINK, V., COX, P. M., FISHER, V., FOLEY, J. A., FRIEND, A. D., KUCCHARIK, C. J., LOMAS, M. R., RAMANKUTTY, N., STICH, S., SMITH, B., WHITE, A. & YOUNG-MOLLING, C. (2001). Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biology* **7**, 357–373.
- CUNNINGHAM, S. & READ, J. (2003a). Comparison of temperate and tropical rainforest tree species: growth responses to temperature. *Journal of Biogeography* **30**, 143–153.
- CUNNINGHAM, S. C. & READ, J. (2003b). Do temperate rainforest trees have a greater ability to acclimate to changing temperatures than tropical rainforest trees? *New Phytologist* **157**, 55–64.
- CUSACK, D. F., TORN, M. S., MCDOWELL, W. H. & SILVER, W. L. (2010). The response of heterotrophic activity and carbon cycling to nitrogen additions and warming in two tropical soils. *Global Change Biology* **16**, 2555–2572.
- DAVIDSON, E. A. & JANSSENS, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**, 165–173.
- DAVIDSON, E. A., JANSSENS, I. A. & LUO, Y. Q. (2006). On the variability of respiration in terrestrial ecosystems: moving beyond Q₁₀. *Global Change Biology* **12**, 154–164.
- DAVIDSON, E. A., NEPSTAD, D. C., ISHIDA, F. Y. & BRANDO, P. M. (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. *Global Change Biology* **14**, 2582–2590.
- DAVIDSON, E. A., VERCHOT, L. V., CATTANIO, J. H., ACKERMAN, I. L. & CARVALHO, J. E. M. (2000). Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry* **48**, 53–69.
- DIFFENBAUGH, N. & SCHERER, M. (2011). Observational and model evidence of global emergence of permanent, unprecedented heat in the 20th and 21st centuries. *Climatic Change* **107**, 615–624.
- DOUGHTY, C. E. (2011). An *in situ* leaf and branch warming experiment in the Amazon. *Biotropica* **43**, 658–665.
- DOUGHTY, C. E. & GOULDEN, M. L. (2008). Are tropical forests near a high temperature threshold? *Journal of Geophysical Research: Biogeosciences* **113**, G00B07.
- ENQUIST, C. A. F. (2002). Predicted regional impacts of climate change on the geographical distribution and diversity of tropical forests in Costa Rica. *Journal of Biogeography* **29**, 519–534.
- EPRON, D., LE DANTEC, V., DUFRENE, E. & GRANIER, A. (2001). Seasonal dynamics of soil carbon dioxide efflux and simulated rhizosphere respiration in a beech forest. *Tree Physiology* **21**, 145–152.
- ESPELETA, J. F. & CLARK, D. A. (2007). Multi-scale variation in fine-root biomass in a tropical rain forest: a seven-year study. *Ecological Monographs* **77**, 377–404.
- FANG, C. M., SMITH, P., MONCRIEFF, J. B. & SMITH, J. U. (2005). Similar response of labile and resistant soil organic matter pools to changes in temperature. *Nature* **433**, 57–59.
- FAO (2009). Food and agriculture organization, FAOSTAT forestry database 2009. Available at <http://faostat.fao.org>; accessed on 1 November 2010.
- FARNSWORTH, E. J., NUNEZ-FARFAN, J., CAREAGA, S. A. & BAZZAZ, F. A. (1995). Phenology and growth of three temperate forest life forms in response to artificial soil warming. *Journal of Ecology* **83**, 967–977.
- FARQUHAR, G. D., VON CAEMMERER, S. & BERRY, J. A. (1980). A biochemical model of photosynthetic carbon dioxide assimilation in leaves of 3-carbon pathway species. *Planta* **149**, 78–90.
- FEELEY, K. J., WRIGHT, S. J., SUPARDI, M. N. N., KASSIM, A. R. & DAVIES, S. J. (2007). Decelerating growth in tropical forest trees. *Ecology Letters* **10**, 461–469.
- FISHER, J. B. & EWERS, F. W. (1995). Vessel dimensions in liana and tree species of Gnetum (Gnetales). *American Journal of Botany* **82**, 1350–1357.
- GHOLZ, H. L., WEDIN, D. A., SMITHERMAN, S. M., HARMON, M. E. & PARTON, W. J. (2000). Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology* **6**, 751–765.
- GIARDINA, C. P. & RYAN, M. G. (2000). Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* **404**, 858–861.
- GRACE, J., MALHI, Y., LLOYD, J., MCINTYRE, J., MIRANDA, A. C., MEIR, P. & MIRANDA, H. S. (1996). The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. *Global Change Biology* **2**, 209–217.
- GRANT, R. F. & ROCHETTE, P. (1994). Soil microbial respiration at different water potentials and temperatures: theory and mathematical modeling. *Soil Science Society of America Journal* **58**, 1681–1690.
- HARLEY, P., VASCONCELLOS, P., VIERLING, L., PINHEIRO, C. C. D., GREENBERG, J., GUENTHER, A., KLINGER, L., DE ALMEIDA, S. S., NEILL, D., BAKER, T., PHILLIPS, O. & MALHI, Y. (2004). Variation in potential for isoprene emissions among Neotropical forest sites. *Global Change Biology* **10**, 630–650.
- HEDIN, L. O., VITOUSEK, P. M. & MATSON, P. A. (2003). Nutrient losses over four million years of tropical forest development. *Ecology* **84**, 2231–2255.
- HOBBIE, E. A., OLSZYK, D. M., RYGIEWICZ, P. T., TINGEY, D. T. & JOHNSON, M. G. (2001). Foliar nitrogen concentrations and natural abundance of ¹⁵N suggest nitrogen allocation patterns of Douglas-fir and mycorrhizal fungi during development in elevated carbon dioxide concentration and temperature. *Tree Physiology* **21**, 1113–1122.
- HÖGBERG, P. & READ, D. J. (2006). Towards a more plant physiological perspective on soil ecology. *Trends in Ecology & Evolution* **21**, 548–554.
- HOLDRIDGE, L. R. (1967). *Life Zone Ecology*. Tropical Science Center, San José, Costa Rica.
- HOLLAND, E. A., NEFF, J. C., TOWNSEND, A. R. & MCKEOWN, B. (2000). Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: Implications for models. *Global Biogeochemical Cycles* **14**, 1137–1151.
- HOULTON, B. Z., WANG, Y. P., VITOUSEK, P. M. & FIELD, C. B. (2008). A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* **454**, 327–330.
- HUNGATE, B. A., DUKES, J. S., SHAW, M. R., LUO, Y. & FIELD, C. B. (2003). Nitrogen and climate change. *Science* **302**, 1512–1513.
- HUTYRA, L. R., WILLIAM, M. J., SALESKA, S. R., GOTTLIEB, E., DAUBE, B. C., DUNN, A. L., AMARAL, D. F., DE CAMARGO, P. B. & WOFSY, S. C. (2007). Seasonal controls on the exchange of carbon and water in an Amazonian rain forest. *Journal of Geophysical Research* **G03008**, 16 pp.
- IPCC (2007). Summary for policymakers. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. SOLOMON, D. QIN, M. MANNING, Z. CHEN, M. MARQUIS, K. B. AVERYT, M. TIGNOR and H. L. MILLER), pp. 2–18. Cambridge University Press, Cambridge, United Kingdom and New York, New York.

- JOBAGY, E. G. & JACKSON, R. B. (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* **10**, 423–436.
- KIEFT, T. L., SOROKER, E. & FIRESTONE, M. K. (1987). Microbial biomass response to a rapid increase in water potential when dry soil is wetted. *Soil Biology and Biochemistry* **19**, 119–126.
- KIMBALL, B., CONLEY, M. & LEWIN, K. (2011). Performance and energy costs associated with scaling infrared heater arrays for warming field plots from 1 to 100 m. *Theoretical and Applied Climatology* **151**, 1–19.
- KIRSCHBAUM, M. U. F. (2000). Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry* **48**, 21–51.
- KIRSCHBAUM, M. U. F. (2004). Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? *Global Change Biology* **10**, 1870–1877.
- KIRSCHBAUM, M. U. F. (2006). The temperature dependence of organic-matter decomposition—still a topic of debate. *Soil Biology & Biochemistry* **38**, 2510–2518.
- KLEBER, M. (2010). What is recalcitrant soil organic matter? *Environmental Chemistry* **7**, 320–332.
- KNORR, W., PRENTICE, I. C., HOUSE, J. I. & HOLLAND, E. A. (2005). Long-term sensitivity of soil carbon turnover to warming. *Nature* **433**, 298–301.
- KOCH, G. W., AMTHOR, J. S. & GOULDEN, M. L. (1994). Diurnal patterns of leaf photosynthesis, conductance and water potential at the top of a lowland rain forest canopy in Cameroon: measurements from the Radeau des Cimes. *Tree Physiology* **14**, 347–360.
- KÖRNER, C. (2003). Carbon limitation in trees. *Journal of Ecology* **91**, 14–17.
- KUZUYAKOV, Y. (2010). Priming effects: Interactions between living and dead organic matter. *Soil Biology & Biochemistry* **42**, 1363–1371.
- LAURANCE, W. F. (1999). Reflections on the tropical deforestation crisis. *Biological Conservation* **91**, 109–117.
- LAURANCE, W. F., OLIVEIRA, A. A., LAURANCE, S. G., CONDIT, R., NASCIMENTO, H. E. M., SANCHEZ-THORIN, A. C., LOVEJOY, T. E., ANDRADE, A., D'ANGELO, S., RIBEIRO, J. E. & DICK, C. W. (2004). Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* **428**, 171–175.
- LERDAU, M. & KELLER, M. (1997). Controls on isoprene emission from trees in a subtropical dry forest. *Plant Cell and Environment* **20**, 569–578.
- LEWIS, S. L., LLOYD, J., SITCH, S., MITCHARD, E. T. A. & LAURANCE, W. F. (2009a). Changing ecology of tropical forests: evidence and drivers. *Annual Review of Ecology and Systematics* **40**, 529–549.
- LEWIS, S. L., LÓPEZ-GÓZALEZ, G., SONKÉ, B., AFFUM-BAFFOE, K., BAKER, T. R., OJO, L. O., PHILLIPS, O. L., REITSMA, J. M., WHITE, L., COMISKEY, J. A., DJUIKOUO, M. N., EWANGO, C. E. N., FELDPAUSCH, T. R., HAMILTON, A. C., GLOOR, M., HART, T., HLADIK, A., LLOYD, J., LOVETT, J. C., MAKANA, J. R., MALHI, Y., MBAGO, F. M., NDANGALASI, H. J., PEACOCK, J., PEH, K. S. H., SHEEL, D., SUNDERLAND, T., SWAINE, M. D., TAPLIN, J., TAYLOR, D., THOMAS, S. C., VOTERE, R. & WÖLL, H. (2009b). Increasing carbon storage in intact African tropical forests. *Nature* **457**, 1003–U3.
- LEWIS, S. L., MALHI, Y. & PHILLIPS, O. L. (2004). Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* **359**, 437–462.
- LLOYD, J. & FARQUHAR, G. D. (2008). Effects of rising temperatures and [CO₂] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 1811–1817.
- LODGE, D. J., MCDOWELL, W. H. & MCSWINEY, C. P. (1994). The importance of nutrient pulses in tropical forests. *Trends in Ecology & Evolution* **9**, 384–387.
- LOESCHER, H. W., OBERBAUER, S. F., GHOLZ, H. L. & CLARK, D. B. (2003). Environmental controls of net ecosystem-level carbon exchange and productivity in a central american tropical wet forest. *Global Change Biology* **9**, 396–412.
- LUO, Y., MELILLO, J., NIU, S., BEIER, C., CLARK, J. S., CLASSEN, A. T., DAVIDSON, E., DUKES, J. S., EVANS, R. D., FIELD, C. B., CZIMCZIK, C. I., KELLER, M., KIMBALL, B. A., KUEPPERS, L. M., NORBY, R. J., PELINI, S. L., PENDALL, E., RASTETTER, E., SIX, J., SMITH, M., TJOELKER, M. G. & TORN, M. S. (2011). Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Global Change Biology* **17**, 843–854.
- LUO, Y. Q., WAN, S. Q., HUI, D. F. & WALLACE, L. L. (2001). Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* **413**, 622–625.
- VON LÜTZOW, M. & KOGEL-KNABNER, I. (2009). Temperature sensitivity of soil organic matter decomposition—what do we know? *Biology and Fertility of Soils* **46**, 1–15.
- VON LÜTZOW, M., KOGEL-KNABNER, I., EKSCMITT, K., MATZNER, E., GUGGENBERGER, G., MARSCHNER, B. & FLESSA, H. (2006). Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions—a review. *European Journal of Soil Science* **57**, 426–445.
- MASLIN, M., MALHI, Y., PHILLIPS, O. & COWLING, S. (2005). New views on an old forest: assessing the longevity, resilience and future of the Amazon rainforest. *Transactions of the Institute of British Geographers* **30**, 477–499.
- MCGRATH, D. A., COMERFORD, N. B. & DURYEA, M. L. (2000). Litter dynamics and monthly fluctuations in soil phosphorus availability in an Amazonian agroforest. *Forest Ecology and Management* **131**, 167–181.
- MCGRODDY, M. E. & SILVER, W. L. (2011). Biogeochemical cycling in tropical forests. In *Tropical Rainforest Responses to Climatic Change* (eds M. BUSH, J. FLENLEY and W. GOSLING), pp. 315–341. Springer Praxis Books, Berlin, Heidelberg.
- MCKANE, R. B., RASTETTER, E. B., MELILLO, J. M., SHAVER, G. R., HOPKINSON, C. S., FERNANDES, D. N., SKOLE, D. L. & CHOMENTOWSKI, W. H. (1995). Effects of global change on carbon storage in tropical forests of South America. *Global Biogeochem Cycles* **9**, 329–350.
- MEENTEMEYER, V. (1978). Macroclimate and lignin control of litter decomposition rates. *Ecology* **59**, 465–472.
- MEINZER, F. C., ANDRADE, J. L., GOLDSTEIN, G., HOLBROOK, N. M., CAVELIER, J. & JACKSON, P. (1997). Control of transpiration from the upper canopy of a tropical forest: the role of stomatal, boundary layer and hydraulic architecture components. *Plant Cell and Environment* **20**, 1242–1252.
- MEINZER, F. C., ANDRADE, J. L., GOLDSTEIN, G., HOLBROOK, N. M., CAVELIER, J. & WRIGHT, S. J. (1999). Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* **121**, 293–301.
- MEIR, P., GRACE, J. & MIRANDA, A. C. (2001). Leaf respiration in two tropical rainforests: constraints on physiology by phosphorus, nitrogen and temperature. *Functional Ecology* **15**, 378–387.
- MELILLO, J. M., BUTLER, S., JOHNSON, J., MOHAN, J., STEUDLER, P., LUX, H., BURROWS, E., BOWLES, F., SMITH, R., SCOTT, L., VARIO, C., HILL, T., BURTON, A., ZHOU, Y. M. & TANG, J. (2011). Soil warming, carbon, nitrogen interactions, and forest carbon budgets. *Proceedings of the National Academy of Sciences* **108**, 9508–9512.
- METCALFE, D. B., MEIR, P., ARAGÃO, L. E. O. C., MALHI, Y., DA COSTA, A. C. L., BRAGA, A., GONÇALVES, P. H. L., DE ATHAYDES, J., DE ALMEIDA, S. S. & WILLIAMS, M. (2007). Factors controlling spatio-temporal variation in carbon dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the eastern Amazon. *Journal of Geophysical Research* **112**, G04001.
- NAKAMURA, M., MULLER, O., TAYANAGI, S., NAKAJI, T. & HIURA, T. (2010). Experimental branch warming alters tall tree leaf phenology and acorn production. *Agricultural and Forest Meteorology* **150**, 1026–1029.
- NORBY, R. J. & LUO, Y. (2004). Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world. *New Phytologist* **162**, 281–293.
- O'BRIEN, J. J., OBERBAUER, S. F. & CLARK, D. B. (2004). Whole tree xylem sap flow responses to multiple environmental variables in a wet tropical forest. *Plant Cell and Environment* **27**, 551–567.
- OECHEL, W. C., VOURLITIS, G. L., HASTINGS, S. J., ZULUETA, R. C., HINZMAN, L. & KANE, D. (2000). Acclimation of ecosystem CO₂ exchange in the Alaskan Arctic in response to decadal climate warming. *Nature* **406**, 978–981.
- OLIVEIRA, R. S., DAWSON, T. E., BURGESS, S. S. O. & NEPSTAD, D. C. (2005). Hydraulic redistribution in three Amazonian trees. *Oecologia* **145**, 354–363.
- PAN, Y., BIRDSEY, R. A., FANG, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Gais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S. & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science* **333**, 988–993.
- PHILLIPS, O. L., BAKER, T. R., ARROYO, L., HIGUCHI, N., KILLEEN, T. J., LAURANCE, W. F., LEWIS, S. L., LLOYD, J., MALHI, Y., MONTAGUDO, A., NEILL, D. A., VARGAS, P. N., SILVA, J. N. M., TERBORGH, J., MARTINEZ, R. V., ALEXIADES, M., ALMEIDA, S., BROWN, S., CHAVE, J., COMISKEY, J. A., CZIMCZIK, C. I., DI FIORE, A., ERWIN, T., KUEBLER, C., LAURANCE, S. G., NASCIMENTO, H. E. M., OLIVIER, J., PALACIOS, W., PATINO, S., PITMAN, N. C. A., QUESADA, C. A., SALDAS, M., LEZAMA, A. T. & VINCETI, B. (2004). Pattern and process in Amazon tree turnover, 1976–2001. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* **359**, 381–407.
- PHILLIPS, O. L., MARTINEZ, R. V., ARROYO, L., BAKER, T. R., KILLEEN, T., LEWIS, S. L., MALHI, Y., MENDOZA, A. M., NEILL, D., VARGAS, P. N., ALEXIADES, M., CERON, C., DI FIORE, A., ERWIN, T., JARDIM, A., PALACIOS, W., SALDIAS, M. & VINCETI, B. (2002). Increasing dominance of large lianas in Amazonian forests. *Nature* **418**, 770–774.
- RAIGH, J. W., RUSSELL, A. E., KITAYAMA, K., PARTON, W. J. & VITOUSEK, P. M. (2006). Temperature influences carbon accumulation in moist tropical forests. *Ecology* **87**, 76–87.
- REED, S. C., WOOD, T. E. & CAVALERI, M. A. (2012). Tropical forests in a warming world. *New Phytologist* **193**, 27–29.
- ROTSTAYN, L. D. & LOHMANN, U. (2002). Tropical rainfall trends and the indirect aerosol effect. *Journal of Climate* **15**, 2103–2116.
- RUEHR, N. K. & BUCHMANN, N. (2010). Soil respiration fluxes in a temperate mixed forest: seasonality and temperature sensitivities differ among microbial and root-rhizosphere respiration. *Tree Physiology* **30**, 165–176.
- RUSTAD, L. R., CAMPBELL, J. C., MARION, G. M., NORBY, R. N., MITCHELL, M. M., HARTLEY, A. H., CORNELISSEN, J. C., GUREVITCH, J. G. & GCTE-NEWS G.-N. (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.
- RYAN, M. G. (2010). Temperature and tree growth. *Tree Physiology* **30**, 667–668.

- SAGE, R. F. & KUBIEN, D. S. (2007). The temperature response of C-3 and C-4 photosynthesis. *Plant Cell and Environment* **30**, 1086–1106.
- SAUGIER, B., ROY, J. & MOONEY, H. A. (2001). Estimations of global terrestrial productivity: converging toward a single number? In *Terrestrial Global Productivity* (eds J. ROY, B. SAUGIER and H. A. MOONEY), pp. 543–557. Academic Press, New York.
- SAXE, H., CANNELL, M. G. R., JOHNSEN, B., RYAN, M. G. & VOURLITIS, G. (2001). Tree and forest functioning in response to global warming. *New Phytologist* **149**, 369–399.
- SAYER, E. J. (2006). Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews* **81**, 1–31.
- SAYER, E. J., POWERS, J. S. & TANNER, E. V. J. (2007). Increased litterfall in tropical forests boosts the transfer of soil CO₂ to the atmosphere. *PLoS ONE* **2**, e1299.
- SAYER, E. J. & TANNER, E. V. J. (2010). A new approach to trenching experiments for measuring root-rhizosphere respiration in a lowland tropical forest. *Soil Biology & Biochemistry* **42**, 347–352.
- SCHNITZER, S. A. & BONGERS, F. (2011). Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* **14**, 397–406.
- SCHWENDENMANN, L., VELDKAMP, E., BRENES, T., O'BRIEN, J. J. & MACKENSEN, J. (2003). Spatial and temporal variation in soil CO₂ efflux in an old-growth neotropical rain forest, La Selva, Costa Rica. *Biogeochemistry* **64**, 111–128.
- SHARKEY, T. D., WIBERLEY, A. E. & DONOHUE, A. R. (2008). Isoprene emission from plants: why and how. *Annals of Botany* **101**, 5–18.
- SIERRA, J. (2002). Nitrogen mineralization and nitrification in a tropical soil: effects of fluctuating temperature conditions. *Soil Biology and Biochemistry* **34**, 1219–1226.
- SILVER, W. L. (1998). The potential effects of elevated CO₂ and climate change on tropical forest soils and biogeochemical cycling. *Climatic Change* **39**, 337–361.
- SILVER, W. L., LUGO, A. E. & KELLER, M. (1999). Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry* **44**, 301–328.
- SILVER, W. L., THOMPSON, A. W., MCGRODDY, M. E., VARNER, R. K., DIAS, J. D., SILVA, H., CRILL, P. M. & KELLER, M. (2005). Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. *Global Change Biology* **11**, 290–306.
- SOTTA, E. D., VELDKAMP, E., GUIMARAES, B. R., PAIXAO, R. K., RUIVO, M. L. P. & ALMEIDA, S. S. (2006). Landscape and climatic controls on spatial and temporal variation in soil CO₂ efflux in an Eastern Amazonian Rainforest, Caxiua, Brazil. *Forest Ecology and Management* **237**, 57–64.
- STANFORD, G., LEGG, J. O., DZIENIA, S. & SIMPSON, E. C. J. (1975). Denitrification and associated nitrogen transformations in soils. *Soil Science* **120**, 147–152.
- STORK, N. E., BALSTON, J., FARQUHAR, G. D., FRANKS, P. J., HOLTUM, J. A. M. & LIDDELL, M. J. (2007). Tropical rainforest canopies and climate change. *Austral Ecology* **32**, 105–112.
- SUBKE, J. A. & BAHN, M. (2010). On the 'temperature sensitivity' of soil respiration: Can we use the immeasurable to predict the unknown? *Soil Biology & Biochemistry* **42**, 1653–1656.
- SUBKE, J. A., INGLIMA, I. & COTRUFO, M. F. (2006). Trends and methodological impacts in soil CO₂ efflux partitioning: a metaanalytical review. *Global Change Biology* **12**, 921–943.
- THORNLEY, J. H. M. & CANNELL, M. G. R. (2001). Soil carbon storage response to temperature: an hypothesis. *Annals of Botany* **87**, 591–598.
- TOWNSEND, A. R., ASNER, G. P. & CLEVELAND, C. C. (2008). The biogeochemical heterogeneity of tropical forests. *Trends in Ecology & Evolution* **23**, 424–431.
- TOWNSEND, A. R., CLEVELAND, C. C., HOULTON, B. Z., ALDEN, C. B. & WHITE, J. W. C. (2011). Multi-element regulation of the tropical forest carbon cycle. *Frontiers in Ecology & the Environment* **9**, 9–17.
- TULLY, K. & LAWRENCE, D. (2010). Declines in leaf litter nitrogen linked to rising temperatures in a wet tropical forest. *Biotropica* **42**, 526–530.
- VASCONCELOS, S. S., ZARIN, D. J., CAPANU, M., LITTELL, R., DAVIDSON, E. A., ISHIDA, F. Y., SANTOS, E. B., ARAUJO, M. M., ARAGAO, D. V., RANGEL-VASCONCELOS, L. G. T., OLIVEIRA, F. D., MCDOWELL, W. H. & DE CARVALHO, C. J. R. (2004). Moisture and substrate availability constrain soil trace gas fluxes in an eastern Amazonian regrowth forest. *Global Biogeochemical Cycles* **18**, GB2009.
- VITOUSEK, P. M. (1984). Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* **65**, 285–298.
- VITOUSEK, P. M. & FARRINGTON, H. (1997). Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biogeochemistry* **37**, 63–75.
- WANG, Y. P. & HOULTON, B. Z. (2009). Nitrogen constraints on terrestrial carbon uptake: Implications for the global carbon-climate feedback. *Geophysical Research Letters* **36**, L24403.
- WARDLE, D. A., WILLIAMSON, W. M., YEATES, G. W. & BONNER, K. I. (2005). Trickle-down effects of aboveground trophic cascades on the soil food web. *Oikos* **111**, 348–358.
- WAY, D. A. & 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 Physiology* **30**, 669–688.
- WHITE, A., CANNELL, M. G. R. & FRIEND, A. D. (2000). CO₂ stabilization, climate change, and the terrestrial carbon sink. *Global Change Biology* **6**, 817–833.
- WIEDER, W. R., CLEVELAND, C. C. & TOWNSEND, A. R. (2009). Controls over leaf litter decomposition in wet tropical forests. *Ecology* **90**, 3333–3341.
- WIELICKI, B. A., WONG, T., ALLAN, R. P., SLINGO, A., KIEHL, J. T., SODEN, B. J., GORDON, C. T., MILLER, A. J., YANG, S. K., RANDALL, D. A., ROBERTSON, F., SUSSKIND, J. & JACOBOWITZ, H. (2002). Evidence for large decadal variability in the tropical mean radiative energy budget. *Science* **295**, 841–844.
- WILD, M. (2009). Global dimming and brightening: a review. *Journal of Geophysical Research* **114**, D00D16.
- WILLIAMS, M., MALHI, Y., NOBRE, A. D., RASTETTER, E. B., GRACE, J. & PEREIRA, M. G. P. (1998). Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: a modelling analysis. *Plant, Cell and Environment* **21**, 953–968.
- WOOD, T. E. & LAWRENCE, D. (2008). No short-term change in soil properties following four-fold litter addition in a Costa Rican rain forest. *Plant and Soil* **307**, 113–122.
- WOOD, T. E., LAWRENCE, D., CLARK, D. A. & CHAZDON, R. L. (2009). Rain forest nutrient cycling and productivity in response to large-scale litter manipulation. *Ecology* **90**, 109–121.
- WRIGHT, S. J. (2005). Tropical forests in a changing environment. *Trends in Ecology & Evolution* **20**, 553–560.

(Received 5 May 2011; revised 16 April 2012; accepted 23 April 2012)