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Review

Tropical forest responses to increasing atmospheric CO_2: current knowledge and opportunities for future research

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Abstract. Elevated atmospheric CO_2 concentrations (c_a) will undoubtedly affect the metabolism of tropical forests worldwide; however, critical aspects of how tropical forests will respond remain largely unknown. Here, we review the current state of knowledge about physiological and ecological responses, with the aim of providing a framework that can help to guide future experimental research. Modelling studies have indicated that elevated c_a can potentially stimulate photosynthesis more in the tropics than at higher latitudes, because suppression of photorespiration by elevated c_a increases with temperature. However, canopy leaves in tropical forests could also potentially reach a high temperature threshold under elevated c_a that will moderate the rise in photosynthesis. Belowground responses, including fine root production, nutrient foraging and soil organic matter processing, will be especially important to the integrated ecosystem response to elevated c_a. Water use efficiency will increase as c_a rises, potentially impacting upon soil moisture status and nutrient availability. Recruitment may be differentially altered for some functional groups, potentially decreasing ecosystem carbon storage. Whole-forest CO_2 enrichment experiments are urgently needed to test predictions of tropical forest functioning under elevated c_a. Smaller scale experiments in the understorey and in gaps would also be informative, and could provide stepping stones towards stand-scale manipulations.

Additional keywords: carbon storage, CO_2 enrichment, liana, phosphorus, succession, water use efficiency.

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Introduction

The rise in atmospheric CO_2 concentration (c_a) caused by human industrialisation is unprecedented, rapid and ubiquitous. Like all vegetation on earth, tropical forests existed under a c_a less than 300 parts per million (ppm) for at least 800 000 years before the start of the 20th century (Lüthi *et al*. 2008). The c_a rose from 300 ppm early in the twentieth century to 392 ppm in 2011, and projections for intermediate emissions scenarios suggest it could exceed 800 ppm by the year 2100 (Intergovernmental Panel on Climate Change 2011). Because CO_2 is the primary substrate for photosynthesis, this dramatic increase in c_a will undoubtedly affect the metabolism of tropical forests worldwide. The qualitative and quantitative expression of such effects, however, is largely unknown and represents a major source of uncertainty that limits our capacity to understand tropical ecosystem processes, assess their vulnerabilities to climate change and improve their representation in Earth system models.

Tropical forests play a significant role in the global carbon cycle. They contain about half the carbon stored in plant biomass in the terrestrial biosphere and account for about one-third of global terrestrial productivity (Field *et al*. 1998; Malhi and Grace 2000; Roy *et al*. 2001; Beer *et al*. 2010; Pan *et al*. 2011; Saatchi *et al*. 2011). In general, responses to elevated c_a have been studied far less in tropical forests than in temperate forests (Hogan *et al*. 1991; Stork *et al*. 2007; Körner 2009; Luo *et al*. 2011; Leakey *et al*. 2012). This gap in research effort may partly reflect the challenges associated with studying tropical forest communities, given their large stature and biological complexity, and logistical challenges associated with conducting research in tropical environments. Free air CO_2 enrichment (FACE) experiments conducted in temperate forests indicated that enriching c_a to 550 ppm caused a 23% increase in net primary productivity (NPP) compared with that observed at ambient c_a of ~380 ppm (Norby *et al*. 2005), with one experiment showing a subsequent decrease to 9% NPP stimulation caused by limited nitrogen availability (Norby *et al*. 2010). No FACE experiment has been conducted in a tropical forest for comparison so far.

Tropical ecosystems differ from temperate ecosystems in important climatic, edaphic, floristic and ecological attributes, and these are likely to influence how they respond to rising c_a. High tropical temperatures increase the potential for stimulation of net photosynthesis (A) by elevated c_a through suppression of photorespiration compared with predictions for cooler temperate and boreal ecosystems (Farquhar *et al*. 1980; Long 1991). On the other hand, it has been argued that tropical forest plants may be near a high temperature threshold, beyond which A could decline (Doughty and Goulden 2008; Doughty 2011). It is not known how the negative effects of high temperature on A will interact with the positive effects of high c_a. In addition, it is possible that biomass production and the competitive ability of tropical canopy trees are not carbon-limited at the current c_a, such that increasing A may have little influence on overall growth performance (Körner 2003, Körner 2009).

FACE experiments have indicated that nitrogen availability plays an important role in constraining productivity responses to elevated c_a in temperate forests (Norby and Zak 2011). However, nitrogen availability is high in many tropical forests (Hedin *et al*. 2009; Brookshire *et al*. 2012). Phosphorus or some other rock-derived nutrient, rather than nitrogen, could present the primary nutritional constraint on growth responses to elevated c_a in tropical ecosystems (Quesada *et al*. 2010; Vitousek *et al*. 2010).

Shifts in floristic composition due to elevated c_a exposure may also be more important in tropical ecosystems. For example, woody climbing plants (lianas) and potentially N_2-fixing legumes are far more abundant in tropical forests than in temperate forests. Functional type-specific responses in these groups could have significant consequences for tropical forest structure and function under elevated c_a, as could an increasing abundance of light-wooded and relatively short-lived pioneer species.

We explore these issues in more detail below, and highlight the challenges and opportunities associated with tackling them experimentally. Our goal is to provide a framework that can be used to guide future experimental research aimed at understanding how woody plants in tropical forests will respond to rising c_a. Conjecture and speculation are necessary ingredients in this endeavour, due to the relatively small amount of research that has thus far been conducted into tropical forests' responses to elevated c_a.

Effects of elevated c_a on leaf gas exchange

In this section, we discuss the effects of elevated c_a on leaf-level A, typically expressed as CO_2 uptake per unit leaf area per unit of time. For a fixed leaf area index, an increase in A will cause a proportional increase in gross primary productivity (GPP). GPP describes the rate of photosynthetic carbon uptake from the atmosphere by a plant canopy, typically expressed per unit of ground area per unit of time.

Elevated c_a generally causes A to increase in plants that use the C_3 photosynthetic pathway (Lloyd and Farquhar 1996; Drake *et al*. 1997). The overwhelming majority of tropical woody plants use this photosynthetic pathway, with notable exceptions in the genera *Euphorbia* (Pearcy and Troughton 1975) and *Clusia* (Holtum *et al*. 2004). An example of the short-term response of A to c_a is shown in Fig. 1 for a seedling of a C_3 tropical pioneer tree, *Ficus insipida* Willd. (K. Winter, unpublished). The measurements were made under near optimal conditions for photosynthesis in a tropical C_3 plant. Fig. 1 clearly shows the potential for significant increases in A in response to rising c_a.

In principle, the A of tropical woody plants has greater potential to respond positively to elevated c_a than that of plants at higher latitudes, as a result of the higher leaf temperatures associated with tropical climates. Rubisco is the primary carboxylating enzyme in C_3 plants. Competition between CO_2 and O_2 at the active sites of Rubisco causes the enzyme to catalyse the fixation of both of these substrates. Fixation of O_2 by Rubisco leads to the release of CO_2 from mitochondria through the process of photorespiration. As leaf temperature increases, the specificity of Rubisco for fixing CO_2 instead of O_2 decreases and the solubility of CO_2 relative to O_2 also decreases. Therefore, photorespiration increases as a proportion of gross photosynthesis with increasing leaf temperature (Farquhar *et al*. 1980; Long 1991). On the other hand, photorespiration can be suppressed by increasing the concentration of CO_2 relative to that of O_2 around the active sites of Rubisco. The upshot is that there is greater opportunity to increase net CO_2 uptake by suppressing photorespiration at higher temperatures. Further predictions resulting from consideration of Rubisco kinetics that are relevant to tropical forest responses to elevated c_a are: (1) the temperature optimum

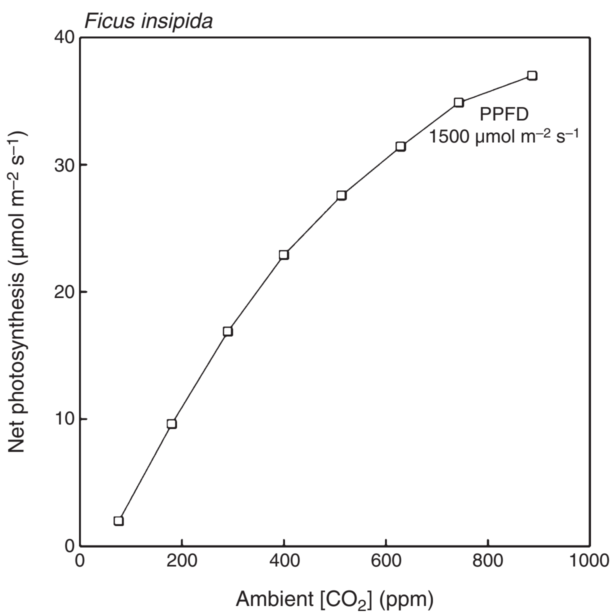

Fig. 1. Net photosynthesis of a leaf of a *Ficus insipida* seedling in response to variation in the CO_2 concentration ($[CO_2]$) of the air surrounding the leaf. Measurements were made at a leaf temperature of 30°C and a photosynthetic photon flux density (PPFD) of 1500 μmol m^{-2} s^{-1} (K. Winter, unpublished).

for A should increase with increasing c_a; (2) the proportional increase in the maximum quantum yield of CO_2 uptake caused by elevated c_a should increase with increasing leaf temperature; and (3) the proportional decrease in the light compensation point caused by elevated c_a should be larger at higher than at lower leaf temperatures (Farquhar *et al*. 1980; Long 1991).

These predictions of the interaction between elevated c_a and temperature at the leaf level are also apparent when A is scaled up to the canopy (Long 1991). As a result, ecosystem models generally predict a larger proportional stimulation of NPP in warm tropical climates, compared with cooler, higher latitudes. For example, a global dynamic vegetation model employing a modified version of the Farquhar *et al*. photosynthesis model (Farquhar *et al*. 1980; Collatz *et al*. 1991) predicted a 35% increase in NPP for tropical forests at c_a of 550 ppm relative to that at c_a of 370 ppm, whereas the predicted increase for temperate forests was 26%. This geographic difference in the simulated proportional stimulation of NPP was largely caused by predicted differences in photorespiration, assuming sufficient nutrient and water availability to support increased NPP (Hickler *et al*. 2008).

On the other hand, the proportional increase in A in response to c_a may be damped if environmental conditions are not otherwise favourable for photosynthetic gas exchange. One reason this might occur is if the stomata close to slow the rate of water loss from leaves. Stomatal conductance (g_s) typically decreases in response to increasing leaf-to-air vapour pressure difference (VPD), and A typically shows a linear or curvilinear relationship with g_s (Wong *et al*. 1979; Cernusak and Marshall 2001; Cernusak *et al*. 2011*a*; Medlyn *et al*. 2011). Thus, a reduction in g_s caused by increased VPD will also cause a reduction in A, with the proportional reduction in A likely to be somewhat less than that in g_s (Farquhar and Sharkey 1982). The VPD can vary as a function of the vapour pressure of the air surrounding the leaf or as a function of the vapour pressure inside the leaf. Because the vapour pressure inside leaves is assumed to be at or near saturation, it is effectively controlled by leaf temperature. Thus, for a fixed vapour pressure outside the leaf, the VPD increases exponentially as leaf temperature increases, and g_s and A are likely to decrease accordingly (Sage and Kubien 2007; Lloyd and Farquhar 2008).

Leaf temperatures in tropical forests are expected to increase with increasing c_a as a result of increasing air temperature and the increasing elevation of leaf temperature above air temperature. Air temperature is expected to increase due to the radiative effects of CO_2 and other greenhouse gases in the atmosphere, and due to decreased evapotranspiration (Sellers *et al*. 1996). Over the last century, the global average surface temperature increased by 0.74°C, accompanying an increase in c_a from 280 ppm to 380 ppm between 1750 and 2005 (Solomon *et al*. 2007). In tropical forest regions, the rate of surface warming since the mid-1970s has averaged 0.26°C per decade (Malhi and Wright 2004). At the leaf level, g_s typically declines in response to elevated c_a (Wullschleger *et al*. 2002; Ainsworth and Rogers 2007), although not always (Körner and Würth 1996; Keel *et al*. 2007). Declining g_s in response to elevated c_a has been observed in seedlings and saplings of tropical tree species (Berryman *et al*. 1994; Goodfellow *et al*. 1997; Cernusak *et al*. 2011*b*). An example of the response of g_s to growth at elevated compared with ambient c_a is shown in Fig. 2*a* for the seedlings of 10 tropical tree species. Here, it can be clearly seen that g_s generally decreased in response to elevated c_a but the response was variable among species. Lower g_s results in a lower transpiration rate (E), causing an increase in leaf temperature (Fig. 3*a*, *b*), with associated increases in VPD (Fig. 3*c*, *d*).

Many tropical forest trees display a pronounced midday depression in both g_s and A on sunny days (Roy and Salager 1992; Koch *et al*. 1994; Zotz *et al*. 1995; Ishida *et al*. 1999; Kosugi *et al*. 2009). This has also been detected at the canopy scale with eddy covariance measurements (Goulden *et al*. 2004; Doughty and Goulden 2008; Kosugi *et al*. 2008). It coincides with the high VPD associated with increasing leaf temperatures under high irradiance (Fig. 4). The midday depression in g_s and A occurs independently of soil moisture status (Kosugi *et al*. 2009). For example, the data shown in Fig. 4 were recorded during the rainy

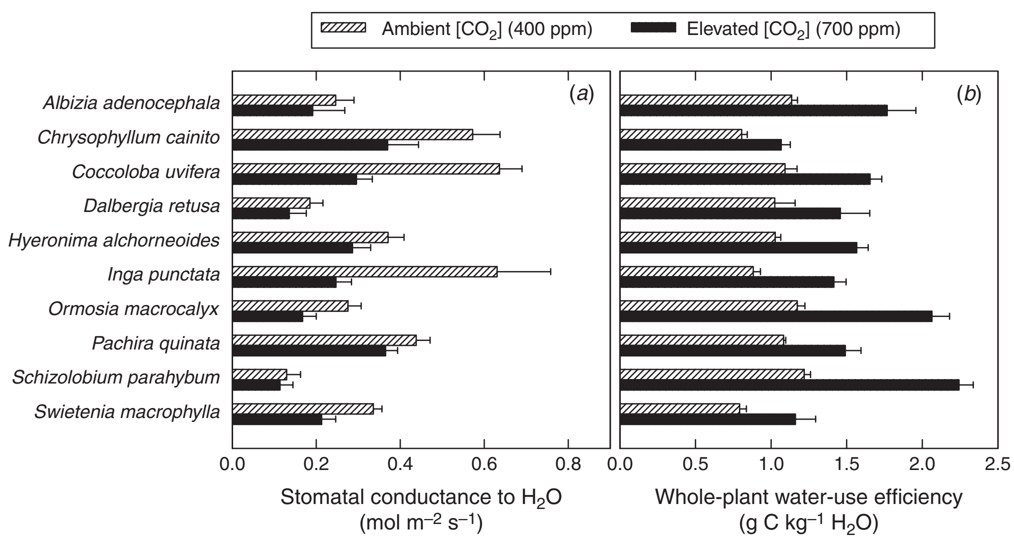

Fig. 2. (*a*) Stomatal conductance and (*b*) whole-plant water use efficiency for seedlings of 10 tropical tree species grown at ambient and elevated CO_2 concentrations ([CO_2]). Data are taken from Cernusak *et al*. (2011*b*).

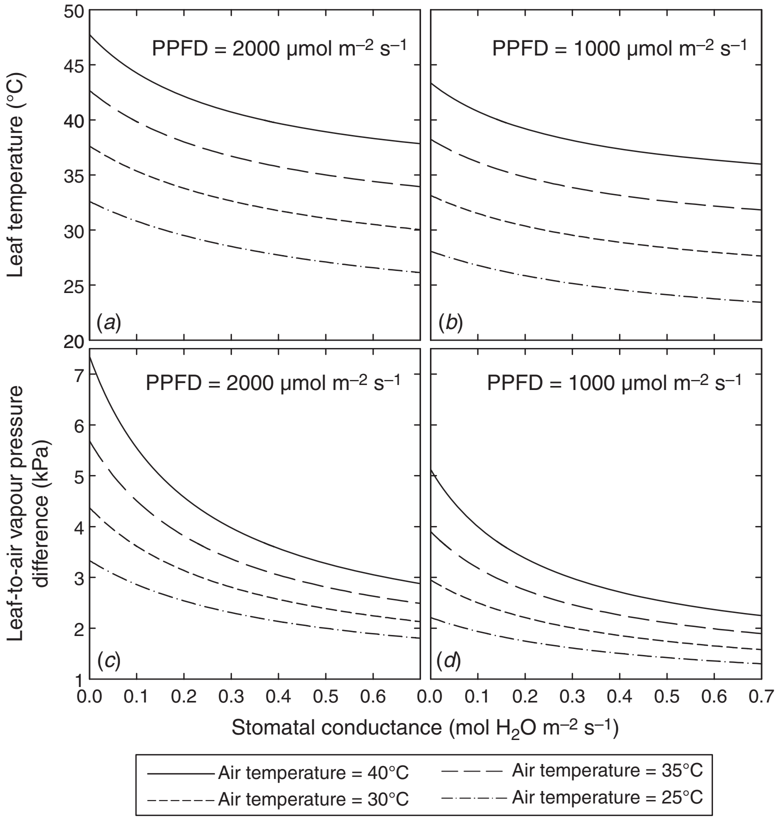

Fig. 3. (*a*, *b*) Predicted leaf temperature and (*c*, *d*) leaf-to-air vapour pressure difference as a function of stomatal conductance at air temperatures ranging from 25°C to 40°C. (*a*, *c*) predictions for an incident photosynthetic photon flux density (PPFD) of 2000 μmol photons $m^{-2} s^{-1}$; (*b*, *d*) predictions for a PPFD of 1000 μmol photons $m^{-2} s^{-1}$. Calculations were performed using leaf energy balance (Campbell and Norman 1998), assuming a relative humidity of 50%, a wind speed of 1.5 m s^{-1} and a leaf width of 10 cm.

season in Panama, when soil moisture was high. Thus, as c_a continues to rise over the coming century, higher VPD caused by higher leaf temperatures could cause midday depressions of g_s and *A* to occur more frequently and for longer periods during the day. This would dampen the positive response of *A* to rising c_a, although an overall increase in *A* is still predicted (Lloyd and Farquhar 2008).

Nonstomatal effects can also limit *A* at high leaf temperatures. The light-saturated potential electron transport rate appears to have a temperature optimum of ~40°C in tropical tree leaves (Lloyd *et al*. 1995; Mercado *et al*. 2006). Thus, *A* would be expected to decrease for a given chloroplastic CO_2 concentration at leaf temperatures higher than 40°C. Exposure to leaf temperatures higher than 45°C can cause denaturation of Rubisco and other photosynthetic enzymes (Berry and Björkman 1980). Necrosis and tissue death typically occur after exposure to leaf temperatures between 50 and 53°C (Krause *et al*. 2010). Sun-exposed outer canopy leaves in a tropical forest reached temperatures between 46°C and 48°C, suggesting they may be operating near their limit of heat tolerance under current conditions (Krause *et al*. 2010).

An *in situ* warming experiment recently demonstrated that *A* in tropical tree and liana leaves was significantly reduced by a warming of 2–3°C over a 13-week period, with the leaf temperatures of warmed leaves reaching 45°C (Doughty 2011). This is within the range of leaf warming that could be expected to occur in response to elevated c_a in the next few decades. The reduction in *A* was attributed mainly to nonstomatal limitations. It has been suggested that elevated c_a could mitigate the adverse effects of elevated temperatures on the photosynthetic performance of tropical tree leaves (Hogan *et al*. 1991) through the suppression of photorespiration and the associated alleviation of photoinhibition under high irradiance (Kriedemann *et al*. 1976; Rasineni *et al*. 2011). Furthermore, the g_s of tropical tree seedlings was observed to decline less in response to increasing leaf temperature for seedlings grown under elevated c_a compared with those grown under ambient c_a (Berryman *et al*. 1994). Thus, elevated c_a has the potential to alleviate both the stomatal and nonstomatal limitations on *A* associated with high leaf temperatures. Future experiments that expose tropical tree leaves to both warming and elevated c_a will be critical for testing this hypothesis further.

Growth under elevated c_a has been shown to cause acclimation of photosynthetic capacity in a range of species, generally explained by reduced Rubisco activity, which is often correlated with reduced leaf nitrogen concentrations (Drake *et al*. 1997). In general, this type of acclimation allows plants to optimise overall performance by balancing sink and source activity. For example, when Rubisco expression is reduced, nitrogen can be reallocated away from the photosynthetic

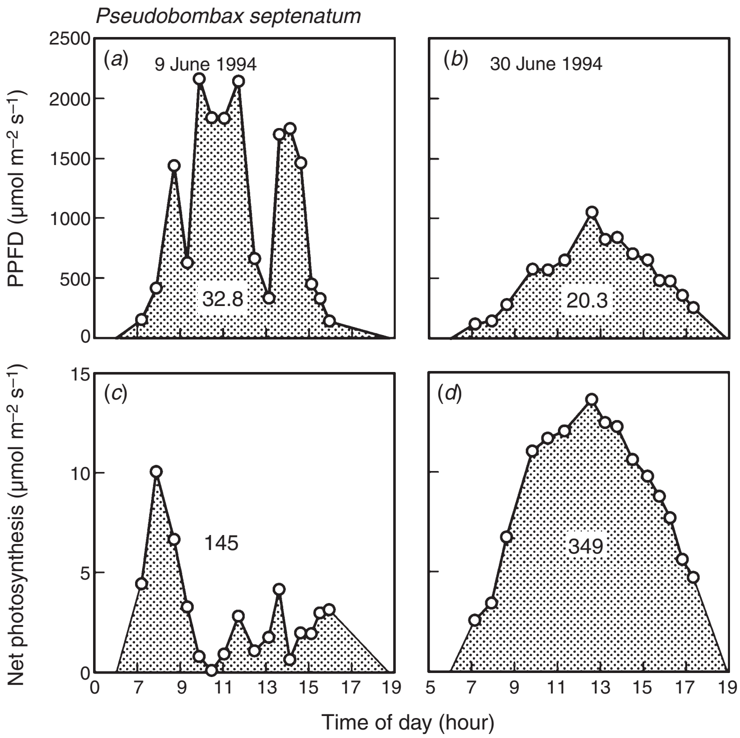

Fig. 4. Net photosynthesis and incident photosynthetic photon flux density (PPFD) of outer canopy leaves of a tall *Pseudobombax septenatum* (Jacq.) Dugand tree in Parque Natural Metropolitano, Republic of Panama, on (*a*, *c*) a sunny day and (*b*, *d*) on an overcast day. (*a*, *b*) PPFD on the 2 days; (*c*, *d*) net photosynthesis. Numbers inside the panels show the summations of the shaded areas under the curves in mol m^{-2} day^{-1} for PPFD and mmol m^{-2} day^{-1} for net photosynthesis (K. Winter, unpublished).

apparatus to structures such as fine roots that allow increased nutrient foraging (Moore *et al*. 1999; Long *et al*. 2004). In FACE experiments with temperate forest trees, the maximum Rubisco carboxylation velocity decreased by ~7% in response to growth at c_a elevated to 200 ppm above ambient CO_2 concentration (Ainsworth and Long 2005). With this lowered photosynthetic capacity, light-saturated photosynthesis was still stimulated by 47% in the elevated c_a treatments. So far, no comparable data have been collected in tropical forest trees.

The above considerations suggest that both stomatal and nonstomatal limitations on *A* will increase with increasing leaf temperatures in tropical canopies, and there is further potential for acclimation or downregulation of photosynthetic capacity to balance source and sink activity. The nature and extent of the interaction between these limitations and the positive effects of elevated c_a on *A* and GPP in tropical forests will have far-reaching consequences for tropical forest function under elevated c_a.

Effects of elevated c_a on growth

NPP is the net amount of carbon fixed into organic matter in a given time after accounting for autotrophic respiration (Eqn 1):

$$NPP = GPP - R_a, \quad (1)$$

where R_a is autotrophic (plant) respiration. NPP can be calculated as the change in plant mass over time plus nonrespiratory carbon losses (i.e. tissue turnover, reproduction, herbivory, exudation of organic compounds from roots, biogenic volatile emissions, etc.), such that NPP = $dM/dt + L$, where *M* is the mass of carbon in a plant or a community of plants, *t* is time, dM/dt is change in mass over change in time, and *L* is nonrespiratory carbon losses (Lloyd and Farquhar 1996). Thus, an increase in NPP may or may not lead to an increase in ecosystem carbon storage in plant biomass (denoted by *M*), depending on how NPP is partitioned between dM/dt and *L*.

From the few datasets so far published, tropical forests appear to function with a relatively low carbon use efficiency (Chambers and Silver 2004; Malhi 2012), defined as the ratio of NPP to GPP. This indicates proportionally high R_a and the potential for a shift in R_a to significantly affect NPP (Metcalfe *et al*. 2010). To date, little is known about whether or how R_a will be affected by elevated c_a in tropical forests. Increasing temperature or increasing supply of respiratory substrates associated with increasing c_a could be expected to cause an increase in maintenance respiration (Leakey *et al*. 2009; Clark *et al*. 2010). On the other hand, responses to temperature may be tempered by acclimation, such that maintenance respiration rates are affected little by a gradual shift in temperature regime (Atkin *et al*. 2005). Nitrogen allocation to tropical tree leaves was observed to decrease under elevated c_a (Berryman *et al.* 1993; Winter *et al*. 2000; Cernusak *et al*. 2011*b*), and this could cause a decrease in leaf maintenance respiration at a given temperature (Ryan 1995; Gonzàlez-Meler *et al*. 2009).

Leaf dark respiration comprises more than a third of total R_a in tropical forests (Chambers and Silver 2004; Cavaleri *et al*. 2008). Not surprisingly, the way R_a is treated in ecosystem models has a large impact on predictions of the tropical forest NPP response to rising c_a, especially with regard to the temperature dependence of R_a (Galbraith *et al*. 2010).

Shifting allocation patterns could affect how the change in biomass over time, d*M*/d*t*, responds to elevated c_a in tropical forests. In artificial tropical miniecosystems, it was observed that *A* nearly doubled under elevated c_a. However, the extra photosynthate produced in the elevated c_a treatment was mostly allocated to increased fine root production and root exudation, thereby increasing *L*, rather than to aboveground biomass and coarse roots, which would have accelerated the increase in *M* (Körner and Arnone 1992). Similar responses were also observed in some temperate ecosystems (Körner *et al*. 2005; Norby *et al*. 2010), as originally foreshadowed by Strain and Bazzaz (1983). Across a broad range of tropical forest plots, a tradeoff was observed between NPP allocation to fine root production versus allocation to wood production, with allocation to the canopy remaining relatively invariant (Malhi *et al*. 2011). This suggests that increased allocation to fine root production under elevated c_a could cause *L* to increase at the expense of increased allocation to the production of long-lived woody tissues, which would cause *M* to increase.

Much of the control over d*M*/d*t* in plants has traditionally been attributed to changes in *A*. This has recently been termed a 'carbon-centric' perspective (Sala *et al*. 2012). Alternatively, it has been suggested that demand for photosynthate at the sites of new tissue synthesis could exert greater control over d*M*/d*t* than does *A* (Körner 2003). This would require that the carbohydrates produced by *A* in excess of their consumption by anabolic processes must be lost from the plant through R_a or *L*. Under such a scenario, it is also likely that some fraction of the excess photosynthate would accumulate as nonstructural carbohydrates (NSC). Thus, analysis of the NSC concentrations in trees could provide a sensor that indicates carbon shortage or surplus for fuelling anabolic metabolism (Körner 2003). A steady and very high NSC concentration would indicate that the current level of *A* provides either a fully adequate supply or an oversupply of reduced carbon compounds to the plant.

In a seasonal forest in Panama, NSC concentrations were observed to be steady through the year or to increase during the dry season (Newell *et al*. 2002; Würth *et al*. 2005). This was interpreted to suggest that d*M*/d*t* was not limited by *A* (Körner 2003; Würth *et al*. 2005). Increasing c_a around the canopy leaves at the same site led to increases in *A* and in NSC concentrations (Würth *et al*. 1998*b*; Lovelock *et al*. 1999), but did not affect the growth rates of branches. This further reinforced the idea that growth will not respond to increased *A* in these trees, although increased growth in the season following exposure to elevated c_a could not be ruled out (Lovelock *et al*. 1999). This interpretation was not supported by the results of another experiment at the same site, in which supplemental lighting was provided to canopy trees under cloudy skies. In that case, growth increased, which was driven by increases in *A* (Graham *et al*. 2003). A definitive test of the hypothesis will require longer-term experiments on woody species growing under elevated c_a in tropical forests.

It was recently suggested that NSC may play an important physiological role in maintaining the integrity of the vascular system of large woody plants (Sala *et al*. 2012). It was also suggested that increased allocation to the NSC pool may be a general response to stress, indicating more severe carbon limitation to growth, rather than *vice versa* (Wiley and Helliker 2012). Further, high soluble sugar concentrations in the leaves may improve their ability to photosynthesise at high temperatures (Hüve *et al*. 2006). If these assertions are correct, there may not be a direct negative relationship between the size of the NSC pool and the ability of tropical trees and lianas to increase growth in response to elevated c_a. On the other hand, if NSC concentrations are generally high, and this reflects an oversupply of carbon for growth such that growth will not respond to a stimulation of *A* (Körner and Arnone 1992; Bader *et al*. 2010), this should be incorporated into coupled climate–carbon models, which treat carbon reserve pools very simply, if at all.

Growth at low nutrient availability consistently reduces the percentage growth response to elevated c_a (McMurtrie *et al*. 2008). This pattern was demonstrated in experiments with seedlings of many tropical tree species (Oberbauer *et al*. 1985; Reekie and Bazzaz 1989; Ziska *et al*. 1991; Lovelock *et al*. 1998; Winter *et al*. 2000; Winter *et al*. 2001*a*, 2001*b*; Cernusak *et al*. 2011*b*; de Oliveira *et al*. 2012), although some exceptions also occurred (Körner and Arnone 1992; Arnone and Körner 1995; Carswell *et al*. 2000). Overall, it is likely that nutrient availability will play a major role in determining the productivity responses of woody tropical forest plants to rising c_a.

Nitrogen appears to be relatively abundant in tropical forests, as indicated by high rates of nitrogen loss (Hedin *et al*. 2009; Brookshire *et al*. 2012) and increasing rates of long-term atmospheric nitrogen deposition (Chen *et al*. 2010; Hietz *et al*. 2011). However, vast areas of tropical forests occur on old, stable landscapes (e.g. large parts of South America, Africa, South-East Asia and Australia). In these regions, severely phosphorus-impoverished soils, a result of prolonged weathering in moist climates (Lambers *et al*. 2008), present a major constraint on plant growth (Vitousek *et al*. 2010). It was recently demonstrated that total soil phosphorus status was the measure of soil fertility that best predicted variation in productivity across a wide range of Amazonian forest plots (Quesada *et al*. 2012). In addition to low phosphorus availability in tropical soils, an apparent link between transpiration and phosphorus acquisition may further diminish the concentrations of phosphorus in plant tissues as c_a rises (Cernusak *et al*. 2011*c*). On the other hand, it has been argued that phosphorus availability and uptake could be maintained under rising c_a by the strong buffer power of soils for inorganic phosphorus, and by increased carbon allocation to mycorrhizal fungi and other specialised mechanisms for phosphorus acquisition (Lovelock *et al*. 1996; Lloyd *et al*. 2001; Lloyd and Farquhar 2008; Turner 2008). Organic phosphorus is abundant in tropical forest soils (Johnson *et al*. 2003; Vincent *et al*. 2010; Turner and Engelbrecht 2011) and may further support any increased growth of tropical forest trees under elevated c_a.

Although phosphorus is likely to be the nutrient that constrains productivity in tropical forests in general, it is also worth pointing out that considerable heterogeneity exists across the tropical biome such that other nutrients can also be limiting. For example, nitrogen appeared to limit productivity in tropical forests on very young and very old soils (Fyllas *et al*. 2009; Mercado *et al*. 2011), in recently established secondary forests (Davidson *et al*. 2007) and in tropical montane forests (Tanner *et al*. 1998). Recent research has shown that the capacity for nitrate assimilation in the shoots of C_3 plants decreases under elevated c_a as a result of decreased photorespiration (Rachmilevitch *et al*. 2004; Bloom *et al*. 2012). If this pattern extends to woody tropical forest plants, the limitations imposed on tropical forest productivity by nitrogen availability could increase. Other nutrients may also play important roles in regulating productivity in tropical forests, for example, calcium, molybdenum and potassium (Vitousek 1984; Barron *et al*. 2009; Wright *et al*. 2011), and their availability could also constrain productivity responses to elevated c_a.

It is clear that there are many unresolved issues associated with predicting whether and to what extent tropical forest NPP will be stimulated by future increases in c_a. Tropical field experiments are urgently needed to address these issues (Leakey *et al*. 2012).

Effects of elevated c_a on resistance to drought

Both seasonal and interannual droughts significantly impact upon the productivity and species composition of tropical forests (Condit *et al*. 1995; Engelbrecht *et al*. 2007; Nepstad *et al*. 2007; Brando *et al*. 2008; Phillips *et al*. 2009; da Costa *et al*. 2010). Elevated c_a could make woody tropical forest plants more able to withstand drought in two ways. First, elevated c_a could increase water use efficiency (WUE), thereby allowing a greater amount of photosynthesis for a given amount of water transpired to the atmosphere (Eamus 1991; Winter *et al*. 2001*a*; Battipaglia *et al*. 2013). This could lead to a reduction in soil water depletion due to reduced canopy-scale transpiration, which could sustain transpiration, and therefore photosynthesis, for a longer time between rain events (Morgan *et al*. 2004; Keel *et al*. 2007; Leuzinger and Körner 2007; Holtum and Winter 2010; Leuzinger and Körner 2010; Macinnis-Ng *et al*. 2011). Such water savings could also facilitate microbial activity and nutrient provision, and enable turgor pressure in meristem tissues to remain above the critical threshold required for cell expansion (Boyer 1968; Eamus *et al*. 1995), thereby facilitating growth. Second, elevated c_a could increase the NSC pool, which, in turn, could be used to sustain plant metabolism for longer periods following stomatal closure and cessation of A in response to drought, according to the carbon-centric perspective (Sala *et al*. 2012).

Because A tends to increase under elevated c_a for a given g_s, leaf-level WUE typically increases. Leaf-level WUE can be defined as the ratio of photosynthesis to transpiration, A/E. A/E can be defined as the ratio of the diffusion gradient for CO_2 to that for water vapour between the external air and the intercellular air spaces in the leaf (Farquhar and Richards 1984):

$$\frac{A}{E} = \frac{c_a\left(1 - \frac{c_i}{c_a}\right)}{1.6VPD}, \quad (2)$$

where c_i is the intercellular CO_2 concentration. The factor 1.6 in the denominator is the ratio of the diffusivity of water vapour to that of CO_2 in the stomatal pores. Eqn (2) shows that if c_i/c_a remains constant, A/E will increase proportionally with increasing c_a, so long as VPD is also constant. If VPD also increases as c_a increases, as suggested above, this will damp the response of A/E to increasing c_a (Barton *et al*. 2012). Variation in c_i/c_a in response to elevated c_a can be assessed instantaneously by measuring changes in the CO_2 and water vapour concentrations of air passing over a leaf (von Caemmerer and Farquhar 1981). In addition, time-integrated assessments of $c_i : c_a$ can be obtained by measuring carbon-isotope discrimination ($\Delta^{13}C$) in plant biomass (Farquhar *et al*. 1982). Although Eqn (2) applies at the leaf level, the increase in WUE under elevated c_a is also manifested at the whole-plant level, as shown in Fig. 2*b* for seedlings of 10 tropical tree species.

Measurement of $\Delta^{13}C$ provides an opportunity to examine the historical responses of c_i/c_a to increasing c_a in tropical trees since preindustrial times. This can be accomplished by analysing $\Delta^{13}C$ in tree rings or in leaf dry matter preserved in herbaria. The few studies conducted so far on tropical trees show that c_i/c_a tended to remain constant as c_a increased from preindustrial to present concentrations (Hietz *et al*. 2005; Nock *et al*. 2011; Bonal *et al*. 2011; Loader *et al*. 2011), or that c_i/c_a decreased in a tropical dry forest tree species (Brienen *et al*. 2011). Both trends (constant c_i/c_a and decreasing c_i/c_a), would indicate large increases in A/E as c_a increased from 280 ppm to 380 ppm if VPD also remained constant. However, historical changes in VPD are more difficult to determine. As noted above, decreasing g_s in response to increasing c_a should lead to an increase in leaf temperature associated with a decrease in evaporative cooling of the leaf by transpiration (Fig. 3). This could lead to an increase in VPD, which would then dampen the increase in A/E caused by increasing c_a. Overall, it seems likely that A/E has increased over the past century and will continue to increase as c_a increases. This suggestion is consistent with the response of whole-plant WUE to elevated c_a, as shown in Fig. 2*b*, because the whole-plant response incorporates the increase in VPD associated with lower g_s.

It is critical to determine how stomatal responses to c_a and VPD are likely to influence evapotranspiration, cloud formation and precipitation patterns in tropical regions as c_a rises. At the continental scale, an increase in WUE in tropical forests could have important implications for the hydrological cycle, including increased runoff (Gedney *et al*. 2006). If WUE increases more than NPP, excess water is likely to enter riverine systems. This could accelerate weathering processes and the export of sediments and associated nutrients to the ocean. Conversely, a decrease in the amount of water returned to the atmosphere by transpiration could cause a decrease in cloud formation and precipitation (Betts *et al*. 2004). Models provide an opportunity to investigate this complex web of feedback over decadal to centennial time scales (Luo *et al*. 2011). Assessment of historical changes in c_i/c_a through analyses of $\Delta^{13}C$ and experimental investigations of the responses of g_s and c_i/c_a to elevated c_a provide a means to parameterise or constrain such models (Buckley 2008; de Boer *et al*. 2011; Prentice *et al*. 2011).

Growth under water deficit generally causes NSC concentrations to increase, and this may be because cell expansion is more sensitive to water stress than is A (Hsiao 1973; Chaves *et al*. 2003; Muller *et al*. 2011). This, combined with the considerations described above, led Körner (2009) to predict that for tropical trees, 'CO_2 would have few if any effects under periodic drought, given the tendency for growth to be controlled by carbon sinks when water is in short supply.' This prediction is based on the idea that the NSC pool represents a passive overflow or repository for carbon supply. However, it has been shown experimentally that growth can respond to elevated c_a under water deficit in tropical tree seedlings (Cernusak *et al.* 2011*b*). Seedlings of two tropical tree species were grown at ambient and elevated c_a, and at a volumetric soil water content of 0.27 or 0.08 $m^3 m^{-3}$. The low water supply was sufficient to reduce g_s to less than half that observed at high water supply. The percentage increase in plant biomass caused by growth at elevated compared with ambient c_a was larger on average for the plants grown under water deficit than for the well-watered plants. This agrees with the results obtained for temperate woody plant seedlings and saplings, which also showed positive growth responses to elevated c_a under water deficit (Tolley and Strain 1984; Arp *et al.* 1998; Centritto *et al.* 1999), although not in every case (Guehl *et al.* 1994; Duursma *et al.* 2011).

The size of the NSC pool in plants generally increases in response to elevated c_a (Drake *et al.* 1997; Ainsworth and Long 2005). There has recently been debate about whether drought-induced tree mortality in the absence of biotic agents results from carbon starvation, hydraulic failure, impaired carbon translocation or a combination of these processes (McDowell *et al.* 2008; Sala *et al.* 2010; Anderegg *et al.* 2012). To the extent that drought-induced mortality can be delayed by having a larger reserve of NSC, elevated c_a should allow tropical woody plants to survive for longer periods under drought. On the other hand, this may not be the case in tropical trees with sunlit canopies if NSC storage is already high under present-day c_a (Newell *et al.* 2002; Körner 2003; Würth *et al.* 2005). Thus it may be the heavily shaded individuals in the understorey that benefit most from higher NSC concentrations as c_a rises (Würth *et al.* 1998*a*; Lloyd and Farquhar 2008).

The interaction between potentially increasing drought frequency and intensity in tropical forests and potentially increasing ability to withstand drought under elevated c_a will play a critical role in defining the overall response of carbon cycling in these ecosystems as c_a rises. Increased WUE was one of the most consistently observed responses to elevated c_a in potted tropical tree seedlings (Ziska *et al.* 1991; Eamus *et al.* 1993; Winter *et al.* 2001*a*; Holtum and Winter 2010; Cernusak *et al.* 2011*b*). Experiments are now required to build upon these initial results, involving woody tropical forest plants growing in their native soil environments and exposed to either naturally occurring or experimentally imposed droughts in combination with elevated c_a.

Effects of elevated c_a on species composition

Much uncertainty surrounding the functioning of tropical forests under elevated c_a derives from potential shifts in forest composition. Although it is currently unknown how changes in species regeneration success under elevated c_a will alter the future carbon cycling of tropical forests, the potential effects may be large. For example, spatial variation in species composition within the single forest type of the 50-ha plot on Barro Colorado Island in Panama was associated with variation in standing dry biomass ranging from 180 Mg ha^{-1} to 440 Mg ha^{-1} (Chave *et al.* 2003). In a further analysis of compositional effects on ecosystem function, Bunker *et al.* (2005) showed that a range of potential extinction scenarios influencing tree species with different functional traits could result in declines in carbon storage of up to 70% on Barro Colorado Island. Clearly, the importance of c_a effects on species regeneration success should be recognised and investigated as a critical driver of future carbon cycling.

The largest impact on forest composition and associated carbon storage will arise if forest disturbance regimes are altered. In mature tropical forests, typical adult tree mortality rates are 1–2% of trees dying per year (Lewis *et al.* 2004), with the resulting disturbance to the forest canopy ranging from single treefall gaps to large canopy openings. Tropical forest plant species lie along a continuum from extremely shade-tolerant to absolutely light-demanding (Wright *et al.* 2005). The most shade-tolerant recruit and survive everywhere. The most light-demanding species will only recruit in large forest openings. Whereas small forest disturbances often result in the replacement of canopy trees by slow-growing shade-tolerant juveniles characterised by high wood density and large adult stature, larger disturbances resulting from multiple tree falls favour the initial recruitment of fast-growing, light-demanding pioneer species, generally characterised by a low wood density and a short lifespan (Swaine and Whitmore 1988).

Elevated c_a may influence forest disturbance regimes in three ways. First, elevated c_a may cause forest turnover rates to increase if there is an increase in competition caused by higher resource availability (i.e. CO_2) (Lewis *et al.* 2009*a*; Bugmann and Bigler 2011). Second, increases in surface temperature are expected to result in stronger convectional storms, such as those that propagate across the Amazon basin (Nelson *et al.* 1994; Garstang *et al.* 1998; Knutson *et al.* 2010). Even though these storms are rare events (Gloor *et al.* 2009; Lloyd *et al.* 2009), they can produce canopy blow-downs extending over hundreds to thousands of hectares, resulting in large patches of early successional vegetation (Negron-Juarez *et al.* 2010). Third, more severe or frequent climate anomalies (Timmermann *et al.* 1999; Neelin *et al.* 2006) can result in biome-wide increases in adult tree mortality. These were observed in the Amazon basin following severe drought in 1997 (Williamson *et al.* 2000) and in 2005 (Phillips *et al.* 2009), and are inferred to have also occurred in 2010 (Lewis *et al.* 2011). Depending on the spatial distribution of tree mortality within the stand, these events have the potential to promote the widespread recruitment of pioneer species.

Elevated c_a may also promote the regeneration of pioneer species in the absence of changes in forest disturbance by influencing the competitive balance between early and late successional species in gaps. For small-seeded pioneers, a critical filter to recruitment success is survival through the early establishment phase (Dalling and Hubbell 2002). Germinating seeds and emerging seedlings are particularly susceptible to drought-induced mortality during short dry spells (Engelbrecht *et al.* 2006; Daws *et al.* 2008), and small seedlings can be smothered by falling litter (Dalling and Hubbell 2002). Elevated c_a may promote seedling establishment if it accelerates seedling growth and effectively shortens this vulnerable establishment period or ameliorates the effects of short-term drought by increasing WUE.

Seedlings establishing in newly formed gaps also face competition from pre-existing recruits of shade-tolerant species (advance regeneration) and potentially from adult trees that surround the gap and contribute to the lateral in-filling of the canopy. If seedling growth rates are not constrained by nutrient availability, the higher maximal assimilation rates of pioneers relative to shade-tolerant species should translate to a greater growth stimulation and competitive advantage (Oberbauer *et al*. 1985). This may be amplified by greater stimulation of photosynthesis during sunflecks, which dominate understorey light environments (Leakey *et al*. 2002). Conversely, elevated c_a may intensify competition between pioneer recruits and the advance regeneration. Elevated c_a has been shown to significantly enhance the growth of shade-tolerant seedlings under very low light conditions (Würth *et al*. 1998*a*) and may be expected to also enhance seedling survival. Growth enhancements are also likely to be strong for shade-tolerant liana species that await gap formation to recruit to the canopy (Körner 2009).

Lianas appear to be increasing in tropical forests over recent decades (Phillips *et al*. 2002; Wright *et al*. 2004; Schnitzer and Bongers 2011). This change in the functional composition of tropical forests may be the result of rising c_a (Lewis *et al*. 2009*a*; Schnitzer and Bongers 2011) or other processes such as shifting dynamics of seed dispersal caused by hunting that favours predominantly wind-dispersed lianas over predominantly animal-dispersed trees (Wright *et al*. 2007). Both liana and tree seedlings have been shown to profit from elevated CO_2 when grown in deep shade (Körner 2009). Beneath the canopy, lianas are likely to exhibit better light foraging per unit of carbon gained than tree saplings, due to their flexible growth strategy. This provides a hypothesised mechanism by which lianas could benefit more from elevated c_a than trees (Körner 2009). Should lianas become more vigorous due to a functional type-specific benefit from elevated c_a, this would have far-reaching consequences for carbon storage (Phillips *et al*. 2002). Liana infestations increase tree mortality and suppress tree growth, whereas lianas themselves allocate relatively little biomass to wood.

Woody legumes are both abundant and diverse in tropical forests, especially in the Neotropics and Africa (Gentry 1988; Losos and Leigh 2004; ter Steege *et al*. 2006). Some of these leguminous tree and liana species have the ability to form bacterial nodules on their roots that can fix atmospheric N_2 (de Souza Moreira *et al*. 1992; Sprent 2009). Such species may be able to respond more strongly to elevated c_a than nonfixing species, especially in nitrogen-poor soils (Thomas *et al*. 1991; Tissue *et al*. 1997; Cernusak *et al*. 2011*b*). An ability to acquire nitrogen from the atmosphere may also provide an advantage for phosphorus acquisition by promoting production of nitrogen-rich phosphatase enzymes in roots (Houlton *et al*. 2008). Such enzymes can be bound to root surfaces or released into the rhizosphere to hydrolyse organically-bound phosphorus, making it available for plant uptake (Richardson *et al*. 2005; Turner 2008). On the other hand, a pan-tropical increase in nitrogen deposition (Chen *et al*. 2010; Hietz *et al*. 2011) might limit the relative advantage of legumes over plant species that are incapable of N_2 fixation. In an *in situ* experiment in a tropical forest understorey, a nodulated legume, *Tachigali versicolour* Standl. & L.O.Williams, had a growth response to elevated c_a similar to that of nonlegumes (Würth *et al*. 1998*a*). However, demand for nitrogen is low in plants in deep shade and the benefit of N_2 fixation may therefore be greatest in a gap environment (McHargue 1999; Barron *et al*. 2011). Future experiments on the responses of nodulated legumes to elevated c_a should consider interactions with irradiance.

Increased carbon allocation to reproduction was observed for temperate trees exposed to FACE (Ladeau and Clark 2006; Way *et al*. 2010). Increased reproductive effort under elevated c_a in tropical forests could have important consequences for long-term population dynamics. In addition, increased carbon allocation to short-lived tissues, such as flowers and fruits, would not lead to the same increase in carbon storage as increased allocation to wood. A significant increase in flower production has been observed over 18 years in a tropical forest in Panama (Wright and Calderon 2006). If this pattern is related to increasing c_a, this may portend further increases in carbon allocation to reproduction as c_a continues to rise.

The Late Paleocene–Eocene Thermal Maximum (PETM) was a global warming event that occurred ~56 million years ago, in which the global mean temperature rapidly increased by ~5°C in ~10 000 years (Zachos *et al*. 2003). This global warming event was associated with a large injection of greenhouse gases into the atmosphere and a rise in c_a to ~1000 ppm. The PETM may provide a historic analogue for anthropogenic climate change, although the latter is occurring at a much faster rate. Pollen assemblages in three stratigraphic sections in eastern Colombia and western Venezuela demonstrated an increase in the diversity of tropical woody plants in response to the PETM (Jaramillo *et al*. 2010). Importantly, the PETM was associated with an intensification of the hydrological cycle, which probably resulted in either increased precipitation in the tropics or at least no increase in aridity (Jaramillo *et al*. 2010; Clementz and Sewall 2011). It is not known to what extent similar conditions will prevail as anthropogenic climate change unfolds. Nevertheless, the diversification of tropical woody plants in response to the PETM provides an extremely valuable insight into potential responses of tropical forests to elevated c_a and climate change.

Currently, our ability to predict changes in the species composition of tropical forests under elevated c_a is poor for at least four reasons: (1) temperate ecosystems have been the focus of most of research effort to date; (2) elevated c_a field studies have focussed on even-aged stands where gap dynamics and gap regeneration were absent; (3) many studies of seedlings have featured plants that were isolated from ecological interactions or grown with a disturbed soil–microbe–plant complex; and (4) the traits that drive variation in response to elevated c_a are not well understood in general, particularly in tropical species (Leakey *et al*. 2012; Leakey and Lau 2012).

Effects of elevated c_a on ecosystem carbon storage

Forests have been a significant carbon sink in recent decades, both globally and in the tropics (Lewis *et al*. 2009*b*; Pan *et al*. 2011). Although it is likely that rising c_a has played at least some role in driving the increase in tropical forest biomass (Lewis *et al*. 2009*a*), several other mechanisms may also have contributed. These possibilities include secondary succession on abandoned agricultural lands, recovery from other anthropogenic uses, including timber and fire wood extraction, and increased deposition of limiting nutrients resulting from anthropogenic activities.

Of the carbon stored in tropical forests, more than half is in live biomass (Pan *et al*. 2011). Repeated censuses of forest inventory plots over time have indicated that live biomass is increasing in some old-growth tropical forests. The average annualised change in aboveground biomass (AGB) in 79 plots in African tropical forests was about +0.6 Mg C ha^{-1} per year during the period 1968–2007 (Lewis *et al*. 2009*b*). Similarly, the average AGB change across 59 Amazonian plots was about +0.6 Mg C ha^{-1} per year from the 1980s until the early 2000s (Baker *et al*. 2004). The global terrestrial carbon sink of ~2 Pg C per year for the 1990s (Solomon *et al.* 2007) implies an increase in ecosystem carbon storage of ~0.2 Mg C ha^{-1} per year, if it were spread evenly over the global vegetated land surface. Körner (2009) suggested one could optimistically allow for three times more missing carbon to be located in tropical forests than in extratropical regions. Thus, for a first approximation, the estimated increase in AGB of 0.6 Mg C ha^{-1} per year is seemingly consistent with the carbon balance of the Earth system.

About one-third of carbon stored in tropical forests is in soil organic matter (Pan *et al*. 2011). The mean residence time for soil organic matter is similar to that for live biomass in tropical forests, on the order of 10–15 years (Malhi *et al*. 1999). This differs markedly from high latitude forests, where the mean residence time for soil organic matter can be 10 times longer than that for live biomass. Little is known about how elevated c_a will affect soil carbon storage in tropical forests as c_a rises. Increased NPP under elevated c_a could accelerate the decomposition of soil organic matter through a priming effect, in which increased litter fall provides the carbon that fuels the microbial decomposition of soil organic matter (Sayer *et al*. 2011). However, like other responses of tropical forests to elevated CO_2, soil priming effects appear to be regulated by nutrient availability (Nottingham *et al*. 2013). In general, small changes in soil carbon are difficult to detect, and even the longest manipulative experiments may not provide sufficient time for directional changes to be detected.

FACE experiments conducted with temperate forest trees provide an important source of information to draw upon when considering the likely responses of ecosystem carbon storage in tropical forests in response to rising c_a. In experiments conducted in young forest stands, there was either a sustained increase in AGB through the full course of the experiment (McCarthy *et al*. 2010); or there was a transitory increase in AGB, with the increase restricted to the first few years of the experiment, and an increased allocation to fine root production and increased carbon in the soil (Norby *et al.* 2010). In a 100-year-old deciduous forest 35 m tall, there was no increase in basal area increment during 8 years of FACE (Körner *et al*. 2005). These experiments demonstrate no consistent evidence for sustained increases in temperate ecosystem carbon storage under elevated c_a (Norby and Zak 2011).

Increased NPP caused by elevated c_a could potentially be associated with less carbon storage in tropical forests if species composition shifts in favour of lianas and shorter-lived, faster growing tree species with lower wood density (Phillips *et al.* 2002; Körner 2004; Laurance *et al*. 2004; Körner 2009). The current distribution of AGB and NPP across Amazonia indicates a negative relationship between the two, such that more productive forests tend be of a lower biomass (Malhi *et al*. 2006; Saatchi *et al*. 2011). Higher mortality rates and lower wood density both contribute to the lower AGB in the Amazonian sites with higher NPP (Malhi *et al*. 2006). Liana infestations increase tree mortality (Putz 1984; Ingwell *et al*. 2010), especially of late successional tree species (Schnitzer and Bongers 2011), which have high wood density compared with early successional tree species (Wright *et al*. 2010). Thus, if liana abundance continues to increase and tropical forests continue to become more dynamic under elevated c_a, they may store less carbon as a result. Interestingly, Amazonian forest plots appear to be increasing in dynamism while increasing in AGB (Baker *et al*. 2004; Lewis *et al*. 2004; Phillips *et al*. 2004). Continued monitoring is required to determine whether this is a transient response that will eventually give way to declining AGB following a shift towards a more gap-dominated structure (Malhi 2012).

The future of tropical forest carbon storage under climate change remains a large source of uncertainty in global climate simulations. For the Amazon Basin, uncertainty in future carbon storage results both from variability in climate projections (Salazar *et al*. 2007; Poulter *et al*. 2010*b*) and from uncertainty associated with direct effects of elevated c_a on the productivity and WUE of tropical forests (Lapola *et al*. 2009; Rammig *et al*. 2010). In simulations with the direct effects of increasing c_a on plant physiological processes turned off, both rising temperature and precipitation reduction caused declines in Amazonian forest biomass. However, with direct effects of elevated c_a on plant physiology turned on, rising c_a mitigated much of the climate-driven decline in forest biomass (Galbraith *et al*. 2010). These modelling studies highlight the critical role that experimental research can play in reducing the uncertainty associated with the direct effects of elevated c_a on the physiology of woody tropical forest plants.

Challenges and opportunities for tropical CO_2 enrichment experiments

FACE studies were helpful for extending observations in temperate forests to the forest stand scale, but compromises in experimental design were necessary because the systems were expensive to construct and operate (Norby and Zak 2011). For example, although there is much interest in understanding the carbon cycling responses of intact mature forests, most of the FACE experiments were conducted in young monoculture plantations. An example is shown in Fig. 5*a*, *b*. The one exception, in which mature, temperate forest trees were exposed to elevated c_a (Körner *et al*. 2005), necessarily required a different compromise: a focus on individual trees rather than the whole ecosystem (Fig. 5*c*, *d*). Tropical forests contain large trees and are species-rich. In studies of forest dynamics, representative plots consequently tend to be 1 ha or larger to adequately capture the abundance of co-occurring species. Given the greater stature, diversity and complexity of tropical forests, as well as many infrastructure constraints (e.g. roads, power, CO_2 supply), a FACE experiment will be even more challenging to implement in a tropical forest. This may

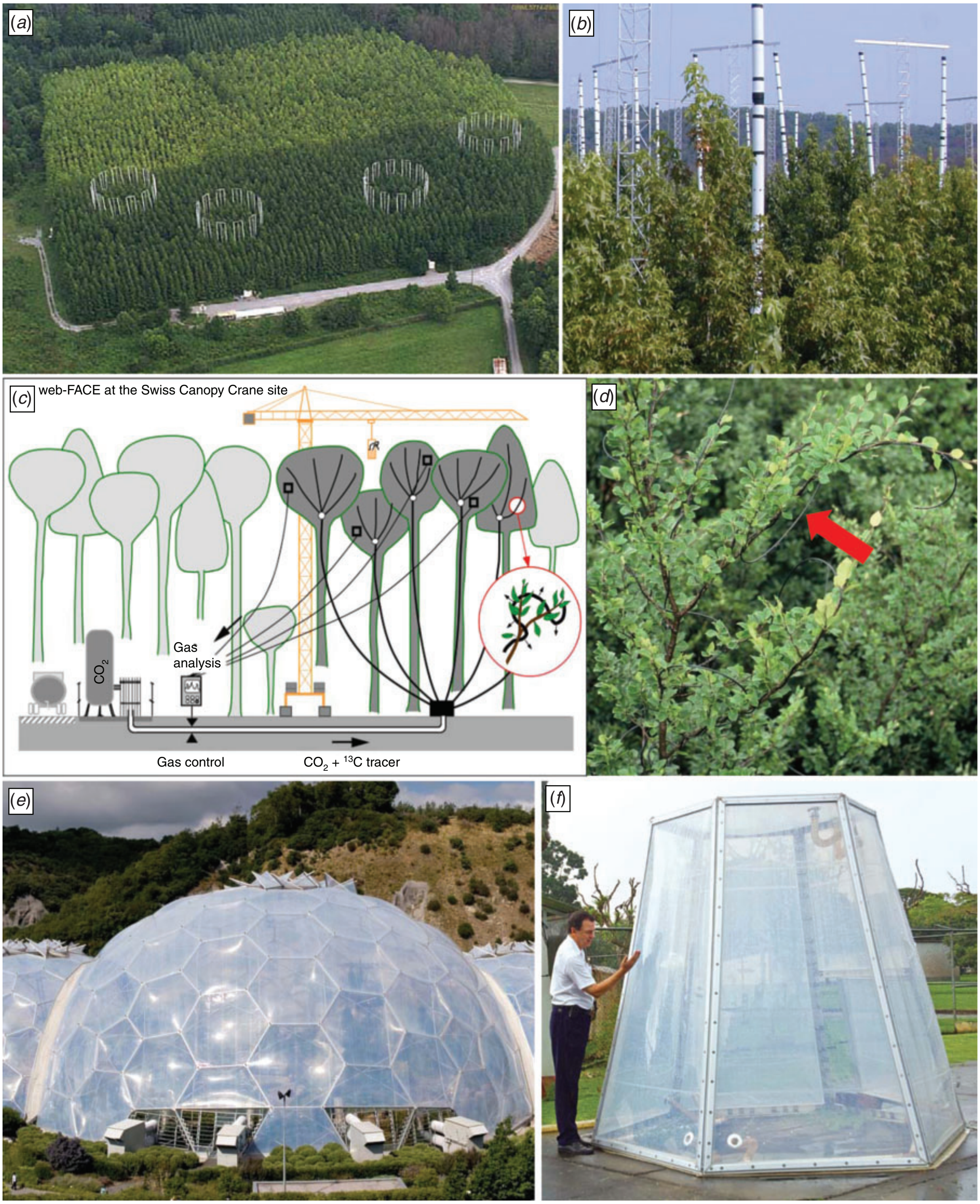

Fig. 5. Some possibilities for stand-scale CO_2 enrichment experiments: (*a*, *b*) free air CO_2 enrichment (FACE) at Oak Ridge National Laboratory; (*c*, *d*) web FACE at the Swiss Canopy Crane site; (*e*) the Eden Project (2013) as an example of a large, naturally-lit enclosure that could accommodate tall forest trees for global change experiments, constructed of ethylene tetrafluoroethylene (ETFE) cushions (credit: Jürgen Matern/Wikimedia Commons, CC-BY-3.0); (*f*) a test of the performance of ETFE cushions in the humid tropics at the Santa Cruz Experimental Field Facility, Smithsonian Tropical Research Institute, Panama. The red arrow in (*d*) points to the tubing used to emit CO_2 in the web FACE experiment.

require the development of new approaches, different from those deployed in previous experiments in temperate forests. Despite these challenges, investigating stand-level responses to elevated c_a in tropical forests must remain a long-term goal, as this is the scale relevant to predicting global climate change feedback over the coming century.

Field experiments to explore how elevated c_a will affect establishment of early and late successional tree species could provide a tractable alternative in the near term, because compositional shifts in tropical forest canopies are likely to be driven by changes in seedling establishment success. Because FACE systems require wind to disperse CO_2 and because wind velocities are often low in forest gaps, CO_2 enrichment systems with forced ventilation, such as simple open-top chambers, would be a suitable tool for the study of gap dynamics, particularly in small treefall gaps. Any such experiment should pay careful attention to soil conditions in order to ensure undisturbed, intact plant–soil interactions. We note that the air within 1–2 m of the forest floor in tropical forests tends to be naturally enriched in CO_2 compared with air above the canopy. However, during the day, when photosynthesis is possible, this natural CO_2 enrichment rarely exceeds 50 ppm (Lloyd *et al*. 1996; Buchmann *et al*. 1997; Würth *et al*. 1998*a*; Holtum and Winter 2001).

Liana responses to elevated c_a in the understorey could be successfully studied using open-top chambers or similar systems for CO_2 augmentation. This type of experiment would further lend itself to differential tests across other plant functional types, for example, comparisons of N_2-fixing tree and liana species with nonfixing species. Multifactor experiments under elevated c_a could also be implemented in the understorey, including variable intensity of drought, irradiance or both. Interactions with irradiance may be particularly important, because elevated c_a can lower the light compensation point in deep shade, with potentially large effects on plant carbon balance under extreme photon shortage.

Tree and liana branches in tropical forest canopies can be exposed to elevated c_a with low-cost installations (Körner and Würth 1996; Würth *et al*. 1998*b*; Lovelock *et al*. 1999) and accessed for physiological measurements using an existing network of tropical forest canopy cranes (Basset *et al*. 2003). In addition, individual leaves or branches can be warmed *in situ* in order to examine responses to both elevated c_a and elevated temperature. Liana responses to elevated c_a along their growth trajectories from the forest floor to the canopy could be successfully studied in this way (Zotz *et al*. 2006). Experiments exposing only a part of the plant to elevated c_a should focus on short-term responses, as interactions at the whole-plant scale will not be present in such experiments. In addition, the degree to which branches behave autonomously in their carbon relations with other parts of the plant could influence physiological responses, and this should be taken into account in experimental design and interpretation of the results (Sprugel *et al*. 1991; Lovelock *et al*. 1999).

The study of forest segments containing tall trees should be feasible in closed systems, a possibility that has been trialled but not extensively exploited in replicated experiments (Osmond *et al*. 2004). Examples of modern, large, naturally-lit enclosures that would accommodate tall forest trees include highly transparent ethylene tetrafluoroethylene covered domes (Fig. 5*e, f*) such as those in the Eden Project (Eden Project 2013). Closed systems would require temperature control, but use relatively little CO_2 for augmentation compared with FACE systems. Moreover, plants can be maintained at above or below current ambient CO_2 conditions. Temperature can also be manipulated. Unlike open CO_2 enrichment systems in which CO_2 concentrations exhibit pronounced short-term fluctuations around the target concentration (Holtum and Winter 2003; Bunce 2012), relatively stable CO_2 concentrations can be maintained in enclosed systems. Although enclosed systems have disadvantages in terms of artificial rain and require sustained air mixing, this technology opens exciting possibilities for experimental ecosystem science, including the measurement of ecosystem gas exchange (Osmond *et al*. 2004), either by placing premanufactured enclosures over existing tropical vegetation or by establishing tree stands in purpose-built enclosures.

Belowground responses, including root deployment and function, nutrient turnover and soil organic matter processing, are especially important to the integrated ecosystem response to elevated CO_2. Belowground processes are difficult to measure and are still poorly quantified. For example, because of the past focus on temperate forests, in which nitrogen is believed to be the major limiting nutrient, there has been little research on the effects of elevated c_a on phosphorus cycling, and phosphorus cycling is poorly represented in models. Experimental approaches and site selection must carefully consider the importance of the belowground environment by avoiding artefacts associated with soil disturbance and include the capability for sufficient belowground measurements.

Many of the critical questions about the role of tropical forests in global carbon cycling are inherently long-term questions (e.g. 50–100 years). Furthermore, no experiment or small set of experiments can ever represent the full diversity of the tropical biome. Models that are well informed by experimental observations offer an opportunity to extrapolate through space and time. Hence an important strategy for designing experiments that will provide the most useful and needed data and the greatest understanding of processes is to engage a modelling perspective from the start.

Opportunities for reducing uncertainty in models

The current generation of ecosystem models demonstrates the potential for elevated c_a to mitigate much of the climate-driven loss of tropical forest biomass that might otherwise occur by the year 2100 (Lapola *et al*. 2009; Galbraith *et al*. 2010; Poulter *et al*. 2010*a*; Rammig *et al*. 2010). However, model predictions are currently based on very limited information and omit what are likely to be critical modifying processes. Uncertainties in the representation of elevated c_a effects on tropical forest vegetation include the potential for elevated c_a to relieve the limitations on canopy photosynthesis caused by high-temperature stress, nutrient limitations on NPP responses to elevated c_a, the effects of elevated c_a on drought induced tree mortality and the effects of elevated c_a on species composition. The results of existing ecosystem models represent testable hypotheses that can guide experimental design, and understanding the critical points of uncertainty in the models with regard to representation of elevated c_a responses can help to identify the highest priority research needs.

Progress can be achieved in the representation of leaf and canopy responses to high temperature by comparing modelled response curves with those observed in leaf cuvettes and by eddy covariance (Lloyd *et al*. 1995; Doughty and Goulden 2008;

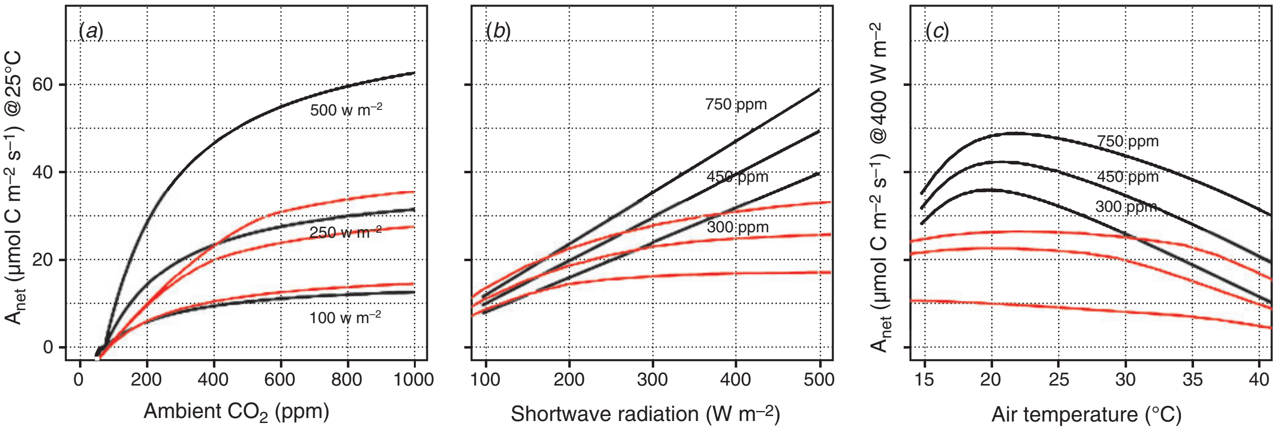

Fig. 6. Theoretical response curves for whole-canopy photosynthesis versus (*a*) ambient CO_2, (*b*) shortwave radiation and (*c*) air temperature using the modified Farquhar *et al.* formulation in the LPJ and ORCHIDEE dynamic global vegetation models (Farquhar *et al.* 1980; Collatz *et al.* 1991; Sitch *et al.* 2003; Krinner *et al.* 2005). Simulations are for a tropical evergreen plant functional type, assuming a nondrought ratio of intercellular CO_2 concentration to ambient CO_2 concentration of 0.80 (LPJ) or 0.67 (ORCHIDEE). Black lines refer to predictions of LPJ and red lines to predictions of ORCHIDEE. Panel (*a*) shows responses at three different irradiances. (*b*) and (*c*) show responses at three different atmospheric CO_2 concentrations.

Verbeeck *et al.* 2011). For example, observations in a tropical forest in Amazonia indicated that a 3°C rise in bulk air temperature above 28.5°C, caused by an increase in irradiance, resulted in a 40% reduction in whole-canopy gross gas exchange (Doughty and Goulden 2008). This was caused by increases in leaf temperatures of 5–8°C in the sunlit fraction of the canopy, and subsequent declines in g_s and A in sunlit leaves. Fig. 6 shows an example of modelled response curves for canopy photosynthesis for two dynamic global vegetation models, Lund-Potsdam-Jena (LPJ) and Organizing Carbon and Hydrology in Dynamic Ecosystems (ORCHIDEE), which differ in their treatment of light diffusion through a canopy, g_s, parameterisation of the Farquhar *et al.* (1980) photosynthesis model and soil–water balance (Sitch *et al.* 2003; Krinner *et al.* 2005). Although temperature and radiation responses differ between the two models, neither appears capable of capturing the pattern observed in the Amazonian forest, namely an almost linear decline in canopy photosynthesis between bulk air temperatures of 28.5 and 31.5°C. In order to extend the representation of temperature responses to elevated c_a conditions, validation data from experimental manipulation experiments are essential.

Recent progress has been made towards including the effects of phosphorus availability in ecosystem models (Lloyd *et al.* 2001; Wang *et al.* 2007; Mercado *et al.* 2011; Goll *et al.* 2012). However, the representation of phosphorus dynamics in models is also limited by uncertainty about the extent to which tropical woody plants can access organic phosphorus, and the mobility of organic phosphorus compounds in tropical forest soils (Turner 2008; Cernusak *et al.* 2011*c*; Turner and Engelbrecht 2011). An improved understanding of phosphorus cycling in tropical forests is needed. Furthermore, the effects of phosphorus availability on the responsiveness of tropical vegetation to elevated c_a have not been tested experimentally. Such experiments should be given a high priority.

Predicting drought-induced vegetation mortality remains a significant challenge (Nepstad *et al.* 2007; McDowell *et al.* 2011). It was recently shown that hydraulic impairment was a better predictor of drought-induced mortality than was the size of the NSC pool in a temperate deciduous tree species (Anderegg *et al.* 2012). Carbon starvation thus did not appear to be a useful predictor. However, if it is shown that the NSC pool plays a significant role in embolism repair (Sala *et al.* 2012), this could have implications for recovery from drought under elevated c_a, because NSC concentrations are likely to increase. Further experimentation is required to develop a mechanistic model of mortality mechanisms and plant age structure that can account for the effects of elevated c_a.

At the community scale, incorporating predictions regarding the effects of elevated c_a on compositional change into ecosystem models represents a further challenge. If experimental manipulations of c_a in tropical forests are limited to targeting juvenile stages, then models will need to upscale observed shifts in the recruitment success of plant functional types to the dynamics of entire forest assemblages. The development of models, such as the Ecosystem Demography model (Moorcroft *et al.* 2001; Medvigy *et al.* 2009; Fisher *et al.* 2010), which link mechanistic representations of ecophysiology and biogeochemistry to the size-structured competition and succession found in forest gap models will provide a potential tool to achieve this integration. In addition, a new approach to representing functional diversity in dynamic global vegetation models was recently developed, based on generating plant traits from distributions of growth strategies rather than from fixed traits (Pavlick *et al.* 2012). This approach could prove useful for simulating tropical forests, allowing for a more flexible representation of their structure and function through space and time. Model validation under ambient c_a using existing long-term tropical forest dynamics data from large plots (Condit 1995) will be essential.

Conclusions

Model simulations suggest that tropical forest NPP will respond more strongly to elevated c_a than that of temperate and boreal forests. This hypothesis could have significant implications for the global carbon cycle and for climate change predictions.

It is sufficiently compelling to justify large-scale investment in experimental testing. Ultimately, we would like to know whether and to what extent elevated c_a-induced increases in NPP in tropical forests will result in increased carbon storage and negative feedback to c_a. Addressing this question will require a combination of experimental and model-based approaches. Additional supporting hypotheses that should also have a high priority for experimental research are the following: (1) elevated c_a will increase the high temperature tolerance of photosynthesis in tropical tree leaves; (2) phosphorus availability will limit tropical forest NPP responses to elevated c_a; (3) elevated c_a will increase the drought resistance of tropical forests; and (4) elevated c_a-induced changes in species composition will cause directional changes in carbon storage in tropical forests.

Carefully considered experiments that need not necessarily take place at the stand scale could make important contributions towards testing these latter hypotheses. Understorey experiments that quantify the potential for elevated c_a to alter the regeneration success of species representing important functional groups, and account for interactions with soil nutrient and water status, would be achievable in the near term and cost-effective. Open-top chambers and branch bags installed in the canopy to elevate c_a, in combination with *in situ* warming, could provide a useful method for answering questions about canopy leaf physiology in relation to temperature and drought. These experiments should not be viewed as replacements for stand-level experiments, but rather as tractable first steps. Stand-level CO_2 enrichment experiments will provide invaluable results, and should be vigorously pursued. The critical role of tropical forests in the terrestrial carbon cycle and the paucity of experimental data so far available together should make tropical forest CO_2 enrichment experiments a very high priority for global climate change research.

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