

# Some aspects of ecophysiological and biogeochemical responses of tropical forests to atmospheric change

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Atmospheric changes that may affect physiological and biogeochemical processes in old-growth tropical forests include: (i) rising atmospheric CO<sub>2</sub> concentration; (ii) an increase in land surface temperature; (iii) changes in precipitation and ecosystem moisture status; and (iv) altered disturbance regimes. Elevated CO<sub>2</sub> is likely to directly influence numerous leaf-level physiological processes, but whether these changes are ultimately reflected in altered ecosystem carbon storage is unclear. The net primary productivity (NPP) response of old-growth tropical forests to elevated CO<sub>2</sub> is unknown, but unlikely to exceed the maximum experimentally measured 25% increase in NPP with a doubling of atmospheric CO<sub>2</sub> from pre-industrial levels. In addition, evolutionary constraints exhibited by tropical plants adapted to low CO<sub>2</sub> levels during most of the Late Pleistocene, may result in little response to increased carbon availability. To set a maximum potential response for a Central Amazon forest, using an individual-tree-based carbon cycling model, a modelling experiment was performed constituting a 25% increase in tree growth rate, linked to the known and expected increase in atmospheric CO<sub>2</sub>. Results demonstrated a maximum carbon sequestration rate of *ca.* 0.2 Mg C per hectare per year (ha<sup>-1</sup> yr<sup>-1</sup>, where 1 ha = 10<sup>4</sup> m<sup>2</sup>), and a sequestration rate of only 0.05 Mg C ha<sup>-1</sup> yr<sup>-1</sup> for an interval centred on calendar years 1980–2020. This low rate results from slow growing trees and the long residence time of carbon in woody tissues. By contrast, changes in disturbance frequency, precipitation patterns and other environmental factors can cause marked and relatively rapid shifts in ecosystem carbon storage. It is our view that observed changes in tropical forest inventory plots over the past few decades is more probably being driven by changes in disturbance or other environmental factors, than by a response to elevated CO<sub>2</sub>. Whether these observed changes in tropical forests are the beginning of long-term permanent shifts or a transient response is uncertain and remains an important research priority.

**Keywords:** net ecosystem exchange; net ecosystem production; climate change; tropical trees; litter decomposition; nutrient limitation

## 1. INTRODUCTION

Atmospheric greenhouse gases are rapidly increasing due to human activities (IPCC 2001a). CO<sub>2</sub> alone represents *ca.* 60% of the total global warming potential of well-mixed greenhouse gases (Hansen *et al.* 1998). A vast amount of research indicates that climate change is an inevitable consequence of increasing greenhouse gases, although the magnitude, timing, precise location and direction of these changes remain uncertain (IPCC 2001b). Considerable effort has been directed towards determining the role of tropical land-use change in the production of CO<sub>2</sub> (Houghton 1991; Fearnside 1997; Fearnside & Barbosa 1998; Houghton *et al.* 2000), but less research has focused on the response of old-growth tropical forests to changes in atmospheric chemistry and climate. Recent work using a network of tropical forest inventory plots demonstrated increases in: (i) tree

recruitment and mortality (Phillips & Gentry 1994); (ii) total tree biomass (Phillips *et al.* 1998); and (iii) climbing woody plant (liana) abundance (Phillips *et al.* 2002). Whether or not these observations are evidence of a response to atmospheric change or a transient phenomenon, is an interesting and important question.

Although climate change in the tropics is often expected to be less than in extra-tropical regions this is not necessarily the case. Wielicki *et al.* (2002) and Chen *et al.* (2002), for example, found larger than expected variations in the tropical atmospheric energy budget, which were associated with El Niño and La Niña (ENSO) events (Hartmann 2002). Stronger and more frequent ENSO events are potential results of increasing greenhouse gases (Timmermann *et al.* 1999; Fedorov & Philander 2000), and ENSO events can have profound effects on tropical precipitation and surface temperature (Holmgren *et al.* 2001). Precipitation in much of the Amazon basin, for example, is appreciably reduced during El Niño and enhanced during La Niña (de Souza *et al.* 2000; Ronchail *et al.* 2002). Perhaps more important than changes in precipitation *per se*, changes in disturbance regimes (e.g. tree mortality) linked to atmospheric change may have marked effects on forest structure and functioning (Condit *et al.*

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1995; Williamson *et al.* 2000; Dale *et al.* 2001). Severe weather events such as hurricanes and powerful storms are expected to increase both in intensity and severity with climate change (Emanuel 1987; Gray 1990). In the Amazon basin, catastrophic blowdowns associated with strong convective storms can raze up to 30 000 ha of forest in a single event (Nelson *et al.* 1994). An increase in the frequency and intensity of these disturbances has the potential to drive large changes in tropical forest structure and functioning.

Processes in the terrestrial biosphere can act as important climate feedback mechanisms, and changing ecological dynamics may be particularly important. Changes in temperature, precipitation and disturbance regimes may result in altered plant community structure and shifts in carbon allocation and storage, which can subsequently impact upon atmospheric CO<sub>2</sub> concentrations. Several studies have explored how atmospheric change may drive community structure, species distribution and ecosystem processes in temperate, boreal and arctic ecosystems (Walther *et al.* 2002), but the response of tropical ecosystems has received much less attention (Enquist 2002). However, research in disturbed areas such as large canopy gaps and forest fragments has demonstrated that species composition and carbon cycling dynamics can change dramatically over relatively short periods (Lugo & Scatena 1996; Laurance *et al.* 1997, 1998a,b; Dale *et al.* 2001).

Forest response to atmospheric change can occur at several different phenomenological scales. Some of the physiological responses of leaves to changes in CO<sub>2</sub> concentration or light intensity, for example, can be almost instantaneous, whereas changes in tree community structure brought about by a gradually shifting climate may take decades to centuries. In addition, some responses may be transient and not reflect long-term ecosystem acclimation. Moreover, not all changes have impacts on forest carbon balance and NEP. For example, photosynthetic carbon assimilation often responds strongly to elevated CO<sub>2</sub>, whereas the corresponding growth response may be considerably less marked or non-existent. Also, carbon allocated to the increased productivity of fast-cycling tissues, such as leaves and fine roots, or to carbohydrate storage and root exudate, may be quickly returned to the atmosphere from autotrophic and heterotrophic respiration, and have little impact on long-term carbon balance. By contrast, changes in carbon allocation to long-lived woody tissues or slow-cycling SOM result in relatively long-term shifts in forest carbon balance (Lloyd & Farquhar 1996; Field 1999; Chambers *et al.* 2001a; Telles *et al.* 2003).

There have been many studies on the effects of elevated CO<sub>2</sub> on physiological, ecological and biogeochemical processes. However, the relevance of most of these studies to old-growth forests remains unclear in many cases, and tropical studies are even more limited (e.g. Würth *et al.* 1998; Winter *et al.* 2001a,b). Elevated CO<sub>2</sub> experiments on plants undergoing stress or changes in resource availability may offer some insight, and studies in natural (unmanaged) ecosystems may be most relevant for understanding tropical forest response. Recently, FACE technology has allowed manipulation of ambient CO<sub>2</sub> concentration while minimizing experimental artefacts (Allen *et al.* 1992), although FACE experiments of forested ecosystems are few (e.g. DeLucia *et al.* 1999;

Norby *et al.* 2001b). Natural CO<sub>2</sub> springs provide additional opportunities to study tree response to lifetime elevated CO<sub>2</sub> exposure (Hättenschwiler *et al.* 1997; Tognetti *et al.* 2000).

This review focuses on the ecophysiological and biogeochemical responses of tropical forests to atmospheric change. We address the following questions. (i) Will tropical forest ecosystems accumulate additional carbon under elevated CO<sub>2</sub>, and if so, at what rate? (ii) How will tropical forests respond to altered disturbance regimes expected under a changing climate? (iii) Is there evidence that tropical forests are already responding to elevated CO<sub>2</sub> or other atmospheric changes? An important consideration is not to predict what the precise changes will be, but to highlight the important processes that may lead to alterations in forest structure and function. Predicting how tropical forests ecosystems will respond to global change is a formidable task, and a synthesis of research on key processes may help provide a foundation for shaping future research priorities. There are relatively few studies on the response of tropical plants and forests to atmospheric change, and thus, in many cases, we are forced to draw on results from numerous extra-tropical studies.

## 2. LEAF GAS EXCHANGE

Predicting the response of tropical forests to elevated atmospheric CO<sub>2</sub> is impeded by the absence of experimental studies for intact tropical ecosystems. Existing elevated CO<sub>2</sub> studies for tropical forest plants are limited to seedlings and saplings (Würth *et al.* 1998) and model communities (Körner & Arnone 1992; Winter *et al.* 2001a,b). Generalizing results from these studies is further confounded by differences in container (pot) size, soil nutrient status and competitive interactions among species. Nevertheless, results from these and innumerable extra-tropical studies have shed considerable light on leaf-level responses to elevated CO<sub>2</sub>, higher temperatures and changes in moisture status.

Photosynthesis responds differently to CO<sub>2</sub> concentration at different temperatures (Farquhar *et al.* 1980). This is primarily due to competitive carboxylation and oxygenation reactions catalysed by Rubisco. The rate of the oxygenation reaction (photorespiration) increases more rapidly than the carboxylation reaction as temperature increases, and CO<sub>2</sub> is also less soluble than O<sub>2</sub> at higher temperatures (Farquhar *et al.* 1980; Farquhar & von Caemmerer 1982; Lambers *et al.* 1998). Thus, under elevated CO<sub>2</sub>, higher temperatures are less inhibitory because the substrate concentration for the carboxylation reaction is proportionally increased. Kirschbaum *et al.* (1994) modelled these direct photosynthetic responses (without additional feedback effects or interactions with water use) and predicted that, compared with rates at pre-industrial CO<sub>2</sub> concentration, photosynthesis in the year 2000 would be *ca.* 20% higher at 35 °C but only 5% higher at 5 °C (see also Grace *et al.* 1996).

One of the most consistent responses of plants to elevated CO<sub>2</sub> is an increase in WUE. Generally, the amount of carbon assimilated per unit water loss (i.e. WUE) increases because stomatal conductance and transpiration are reduced under elevated CO<sub>2</sub>, whereas internal CO<sub>2</sub> concentration ( $C_i$ ) remains relatively constant (but see

Marshall & Monserud 1996), so that more carbon is assimilated at a given transpiration rate (Hsiao & Jackson 1999). Thus, an increase in WUE is similar in some respects to a decrease in water stress (Amthor 1999). The magnitude of this effect, however, is dependent on the experimental conditions. Field *et al.* (1995) found that stomatal conductance was reduced 31% for plants in growth chambers, 17% for plants in open-top chambers and 4% for plants grown in the ground. Furthermore, there are often large species differences in WUE and plant response to drought under elevated CO<sub>2</sub> (Beerling *et al.* 1996). An increase in WUE is probably the most common leaf-level response to elevated CO<sub>2</sub>, although changes in WUE are not necessarily linked with proportional changes in plant growth.

Growth under elevated CO<sub>2</sub> often alters how leaves respond to CO<sub>2</sub>. This is demonstrated by measuring net photosynthesis ( $A$ ) as a function of internal CO<sub>2</sub> concentration ( $C_i$ ) ( $A-C_i$  curves). Both increases and decreases of  $A$  at varying levels of  $C_i$  (down- and upregulation) have been demonstrated (Ceulemans *et al.* 1999; Hsiao & Jackson 1999; Rogers & Ellsworth 2002). When additional carbohydrate can support increased growth, there is a tendency for upregulation, whereas when carbon is assimilated in excess of a plant's ability to initiate new sinks, there is a tendency for downregulation. Also, there appears to be less downregulation in field-grown plants under elevated CO<sub>2</sub> where roots are allowed to explore a larger volume of soil (Stitt 1991; Hsiao & Jackson 1999). For example, Thomas & Strain (1991) demonstrated that downregulated cotton plants improved photosynthetic capacity within 4 days of transfer from small to large pots. In addition, plants experiencing low nitrogen availability often show increased downregulation under elevated CO<sub>2</sub>, but response varies, and additional studies of low nutrient supply are needed to further elucidate complex interactions with other resources and stresses (Hsiao & Jackson 1999). Thus, the physiological response of tropical trees to elevated CO<sub>2</sub> will depend, in part, on opportunities to initiate new sinks. If carbon is assimilated in excess of the capacity to generate new sinks, a decrease in photosynthetic capacity is often the result (Stitt 1991; Amthor 1995; Ceulemans *et al.* 1999). This sink regulation of photosynthesis (Herold 1980; Ng & Hew 1999) may be particularly important in nutrient-deficient tropical forests with a high capacity for carbon assimilation but low carbon use efficiency (Chambers *et al.* 2004a).

Tropical trees often experience midday and post-midday declines in photosynthetic carbon assimilation rates that may be driven by moisture stress (Williams *et al.* 1998). If moisture stress is the causal factor, midday depression may be partly ameliorated under elevated CO<sub>2</sub>, although experimental studies are lacking. However, other factors may also cause reductions in post-midday carbon assimilation rates. For example, photosynthesis is one of the most heat sensitive of plant physiological processes, and temperatures in the range of 35–45 °C tend to inhibit photosynthetic rates (Berry & Björkman 1980). Although the change in mean surface temperature in response to elevated greenhouse gases is expected to be less in the tropics than at higher latitudes, changes in global circulation patterns such as ENSO (Timmermann *et al.* 1999; Fedorov & Philander 2000) can have larger impacts than

expected when considering greenhouse gases alone. The optimum temperature for photosynthesis tends to increase under elevated CO<sub>2</sub>, and many plants are flexible in acclimating to higher temperatures (Berry & Björkman 1980). However, species response to high temperature varies considerably, and studies are needed to determine what species with what characteristics are particularly vulnerable. Because direct solar radiation in the tropics often increases midday leaf temperatures beyond 40 °C (Koch *et al.* 1994; Ishida *et al.* 1999; Kitao *et al.* 2000), protective mechanisms may frequently be invoked, resulting in relatively lowered post-midday photosynthetic rates under environmental conditions that are similar to those that occur during morning hours.

Nutrient availability can also interact with plant responses to elevated CO<sub>2</sub>, particularly in the moist tropics where most soils are highly weathered with low inputs of primary minerals (Sanchez 1976). Growth of tropical plant species increased under high nutrient availability and elevated CO<sub>2</sub> (Körner & Arnone 1992), but not when soil nutrient availability resembled field conditions (Arnone & Körner 1995). Many CO<sub>2</sub> manipulation experiments on individual (potted) tropical plants were conducted under unnaturally high nutrient concentrations (Oberbauer *et al.* 1985; Reekie & Bazzaz 1989; Ziska *et al.* 1991), and results from these studies may not reflect plant response under field conditions. At the same time, elevated CO<sub>2</sub> studies in small pots are often suspected of demonstrating a reduced response due to root growth inhibition (Hsiao & Jackson 1999). However, tropical forest soils often contain high fine-root density (Jackson *et al.* 1996) and below-ground competition is strong. Thus, the response of plants under conditions of high root density may actually be a better reflection of response under field conditions.

Generalizing gas exchange studies performed on individual leaves and plants to canopies and whole forests is problematic (Ehleringer & Field 1993). One issue of particular interest is whether reduced transpiration rates will result in elevated leaf temperatures. Although many studies demonstrate increased WUE per unit leaf area, this may not necessarily result in a reduction in whole forest transpiration rates (Amthor 1999). First, growth in elevated CO<sub>2</sub> can alter leaf size and number with the potential to change ecosystem LAI (Hsiao & Jackson 1999), and there are often interactions between biochemical and morphological responses to elevated CO<sub>2</sub> (Peterson *et al.* 1999). An increase in LAI with a decrease in stomatal conductance may ultimately have no effect on total forest transpiration rate, although in tropical forests where LAI is often high, there may be little room for additional leaf area. Stomatal density also tends to decrease under elevated CO<sub>2</sub>, which can affect ecosystem transpiration rates, although feedbacks with the planetary boundary layer are complex and difficult to predict (Jarvis & McNaughton 1986). Eddy covariance measurements in the Amazon basin show that *ca.* 80% of intercepted net radiation is lost as latent heat and only 20% by convection (Grace *et al.* 1995), demonstrating the importance of leaf cooling by transpiration for tropical trees (Beerling *et al.* 2001). Thus, although reduced whole forest transpiration rates would probably result in elevated leaf temperatures, predicting large-scale transpiration response is neither straightforward nor well understood (Jarvis & McNaughton 1986).

### 3. PLANT RESPIRATION

Two different effects of elevated CO<sub>2</sub> on plant respiration have been suggested and are often referred to as direct (short-term) and indirect (long-term) effects. Although these studies were not performed on tropical plants, many results from extra-tropical studies are probably relevant. First, initial studies indicated that a direct reduction in respiration was caused by inhibition by CO<sub>2</sub> of the activity of a key enzyme (cytochrome *c* oxidase) in the mitochondrial electron transport chain (Gonzalez-Meler *et al.* 1996). However, recent studies suggest that flux control cannot be attributed to enzymatic constraints (Gonzalez-Meler & Siedow 1999; Bunce 2001). It appears that elevated CO<sub>2</sub> has little, if any, direct effect on plant respiration, and that CO<sub>2</sub> effects found in earlier studies were primarily experimental artefacts caused by leaks and other factors (Amthor 1997, 2000; Gonzalez-Meler & Siedow 1999; Amthor *et al.* 2001; Tjoelker *et al.* 2001; Bruhn *et al.* 2002; Jahnke & Krewitt 2002). Nevertheless, Hamilton *et al.* (2001), even after carefully correcting for experimental artefacts, recently found a direct 10% inhibition of night-time leaf respiration by elevated CO<sub>2</sub> (+ 200 p.p.m.v.) for sweetgum trees, although there was no direct inhibition for loblolly pine needles. Although it appears that a consensus is yet to fully emerge on the direct inhibition of plant respiration by elevated CO<sub>2</sub>, the direct effect is probably much less important than suggested in earlier studies.

The indirect (long-term) effects of elevated CO<sub>2</sub> on plant respiration are also contradictory. A recent meta-analysis found that growth in elevated CO<sub>2</sub> reduces leaf (dark) respiration by *ca.* 18% (per unit mass) (Curtis & Wang 1998). However, other studies have found increases or no long-term response of leaf respiration to elevated CO<sub>2</sub> (Amthor 1997; Norby *et al.* 1999; Tjoelker *et al.* 1999; Hamilton *et al.* 2001). The response of woody tissue respiration is also inconsistent. Edwards *et al.* (2002) found that growth and maintenance respiration of woody tissues increased by 23% and 48%, respectively, under elevated CO<sub>2</sub> (×1.4 ambient) in a FACE experiment in a sweetgum plantation. Interestingly, during a 4 day period when CO<sub>2</sub> fumigation was turned off, both stem respiration and sucrose concentrations declined. By contrast, for ponderosa pine growth in open-top chambers, Carey *et al.* (1996) found that only woody tissue maintenance respiration increased under elevated CO<sub>2</sub>, not growth respiration, and the difference was only found above 21 °C. Further contrasting, Janous *et al.* (2000) found slightly less total stem respiration under elevated CO<sub>2</sub> for Norway spruce in open-top chambers.

It appears that the long-term response of plant respiration to elevated CO<sub>2</sub> is complex, and further studies are needed to clarify contradictory results. In ecosystems where wastage (e.g. non-functional, futile cycles, alternative oxidase) respiration is an important process, the response of respiration to elevated CO<sub>2</sub> may be even more complex. For example, in addition to the cytochrome pathway that produces ATP, plants also have an alternative respiratory pathway of questionable utility (Lambers 1982, 1997). Several potential functions of the alternate pathway include (but are not limited to): (i) the production of heat, for example, to attract pollinators to

reproductive organs; (ii) as an overflow in response to excess carbohydrate; (iii) as a way to less efficiently produce ATP in response to low inorganic phosphorus (P<sub>i</sub>); and (iv) to maintain excessive electron transport capacity so that a plant can quickly respond to changes in resource availability. Whereas the cytochrome pathway is regulated by carbohydrate, P<sub>i</sub> and ADP availability, regulation of the alternate respiratory pathway is more complex, and the factors that control its activity are not well understood (Gonzalez-Meler *et al.* 2001).

No studies have looked at how carbohydrate partitioning between the cytochrome and alternate oxidase responds to elevated CO<sub>2</sub>. Because total respiratory efflux comprises construction (R<sub>c</sub>), maintenance (R<sub>m</sub>) and wastage (R<sub>w</sub>) components, studies that consider only R<sub>c</sub> and R<sub>m</sub> may be obscuring relative changes in these key processes. Chambers *et al.* (2004a) found that *ca.* 70% of assimilated carbon was lost as autotrophic respiration for central Amazon trees growing on nutrient-deficient soils. If much of this respiration is non-functional (i.e. R<sub>w</sub>), central Amazon trees may already be capturing carbon in excess of immediate metabolic needs, and may not be particularly responsive to increased carbon availability (Chambers *et al.* 2004a).

### 4. ADAPTIVE AND EVOLUTIONARY CONSTRAINTS

Recent plant exposure to elevated atmospheric CO<sub>2</sub> represents only a small fraction of the past *ca.* 500 000 years when CO<sub>2</sub> levels maintained 180–280 p.p.m.v. (Petit *et al.* 1999). Thus, much of the world's flora is probably adapted to the relatively low CO<sub>2</sub> levels of the Late Pleistocene, and adaptive traits conferring survival at low CO<sub>2</sub> may constrain plants from exploiting increased carbon availability (Sage & Coleman 2001). This evolutionary legacy may have resulted in plants that are overly conservative in terms of stress response, growth potential, allocation patterns and storage investment, and despite the current and expected increase in atmospheric CO<sub>2</sub>, many plants may often respond as if carbon were still a limiting resource (Sage & Cowling 1999).

Owing to substrate limitation and a relative increase in photorespiration under low CO<sub>2</sub>, photosynthetic rates for C<sub>3</sub> species are predicted to have been 20–30% less in the late nineteenth century and 40–60% less during the last glaciation (Sage 1995). Vegetation from tropical regions would have been more negatively impacted because the effect of low atmospheric CO<sub>2</sub> on both photorespiration and substrate limitation are much greater at higher rather than lower temperatures (Sage & Coleman 2001). Also, in the same way that CO<sub>2</sub> enrichment can attenuate the inhibitory effects of other stresses (Amthor 1999; Hsiao & Jackson 1999), CO<sub>2</sub> depletion can aggravate stresses (Sage 1995), and these stresses may have been heightened in many tropical trees. Conditions that are not harmful today may have been unfavourable under lower CO<sub>2</sub>, and if these conditions increased the probability of mortality, they may have acted as strong selective pressures (Sage & Cowling 1999). Thus, although temperature and moisture stresses are expected to be relieved under elevated CO<sub>2</sub>, owing to evolutionary constraints, many plants may be conservative in response to this relief. Tropical tree species may exhibit particularly conservative adaptations conferring

elevated photosynthetic capacity and more carbohydrate storing mechanisms than needed under elevated CO<sub>2</sub>.

Tropical trees often experience several environmental and ecological stresses including chronically low nutrient availability, strong seasonal variability in precipitation, large diurnal changes in leaf temperature and plant water status, and intense competition for resources with other plants. Some of these stresses may have been aggravated during recent geological time. In addition to lower atmospheric CO<sub>2</sub>, for example, precipitation may have been reduced in many tropical regions during Pleistocene glaciations (Vanderhammen & Absy 1994; Mora & Pratt 2001). Given these conditions of the evolutionary past, how might tropical trees have adapted to effectively balance the acquisition of numerous resources with differing availabilities? In general, plants living under stressful conditions often acquire limiting resources in excess of metabolic needs, and then exploit these stored resources during stressful periods (Chapin 1980; Mooney & Chiariello 1984; Bloom *et al.* 1985). Plant response to stress involves complex interactions among resource availabilities and acquisition strategies under the prevailing conditions (Grime 1988; Tilman 1993) and these responses may be maladaptive under changing conditions (Sage & Cowling 1999).

Tree species employ several strategies for coping with drought in seasonally dry tropical forests, and many of these involve maintaining adequate carbohydrate reserves. This is readily apparent in a marked annual periodicity of leaf production and senescence. Although the exact mechanisms that drive these phenological patterns are uncertain (Wright & Cornejo 1990; Wright & Van Shaik 1994; Reich 1995), they are clearly timed to avoid drought stress and take advantage of more favourable conditions as the rainy season begins. For example, several species are drought deciduous with a leaf flush that occurs at the end of the dry season (Wright 1996). Yet other canopy tree species have different leaf phenotypes produced at the beginning and end of the wet season, the latter of which may be adapted for reducing moisture stress by increasing WUE (Mulkey *et al.* 1992; Kitajima *et al.* 1997). In both cases, sufficient carbohydrate reserves are required to produce a new crop of leaves, and to maintain minimal metabolic rates when moisture stress is severe or the canopy is leafless, and these allocation strategies may not vary even when stress is relieved. For example, Wright & Cornejo (1990) irrigated plots in a Panamanian forest during the four month dry season and found that, for most species, the timing of leaf fall did not differ between manipulated and control plots, indicating that plant water status is rarely the proximal cue for leaf fall. Similarly, phenological patterns of growth and resource allocation may not be particularly responsive to stress relief associated with elevated CO<sub>2</sub>.

Similar to seasonal changes in carbon acquisition strategies, many tropical trees probably maximize carbon gain early in the day before midday leaf temperatures rise and leaf water potential declines to potentially harmful levels. Midday moisture and temperature stress increases the degree to which carbon is a limiting resource (Koch & Mooney 1996) and these diurnal responses may also have been heightened under a Pleistocene climate. Although these midday stresses may be alleviated under elevated CO<sub>2</sub>, many plants may be responding to other cues (e.g. vapour pressure deficit, temperature), and respond

conservatively. Perhaps the high carbohydrate storage demonstrated in some studies at the current atmospheric CO<sub>2</sub> indicates that many plants already maintain excessive photosynthetic capacity (Gifford & Evans 1981; Stitt 1991; Stitt & Schulze 1994). Excessive carbohydrate accumulation under elevated CO<sub>2</sub> may also invoke novel stresses, including carbohydrate toxicity (Ehret & Jolliffe 1985; Stitt 1994).

Many tropical tree species may be adapted to minimize water loss and maximize carbon gain and storage for use during stressful periods. Under 180–280 p.p.m.v. CO<sub>2</sub> of the Pleistocene, WUE would have probably been reduced (Amthor 1999), and during these times, variation in WUE and allocation strategies may have conferred differential success in species adaptation (Hsiao & Jackson 1999). Numerous elevated CO<sub>2</sub> studies in natural and simulated plant communities show little or no increase in growth despite large increases in photosynthetic rates, WUE and the level of carbohydrate storage (Bazzaz 1990; Koch & Mooney 1996). To avoid stresses associated with CO<sub>2</sub> depletion during the Pleistocene, genetically fixed limits on growth rate restricting competition between new tissue production and storage, ensuring adequate carbohydrate reserves during stress conditions, may have been advantageous (Sage & Cowling 1999). Developmental controls over maximum meristematic activity may restrict the growth potential for many tropical tree species, limiting growth even when carbon is abundant.

## 5. NET PRIMARY PRODUCTIVITY

Although many studies show an increase in productivity under elevated CO<sub>2</sub>, the magnitude of this response is often dependent on the experimental conditions. First, changes in productivity found under elevated CO<sub>2</sub> are usually smaller and more variable than stimulation of leaf photosynthesis (Koch & Mooney 1996; Sage & Cowling 1999). Second, enhanced productivity is generally lower for natural as compared with managed ecosystems (Field 1999). Third, productivity stimulation is often reduced under conditions of low soil nutrient supply (Kirschbaum *et al.* 1994; Curtis & Wang 1998), although stimulation may be enhanced under low water supply (Poorter & Perez-Soba 2001). Winter *et al.* (2000) found that biomass accumulation for a model community of two species grown in open-top chambers in a forest clearing in Panama was not significantly affected by elevated CO<sub>2</sub>. By contrast, with the addition of large amounts of fertilizer (Winter *et al.* 2001b), biomass accumulation was enhanced by more than 50%. Although much has been gained from elevated CO<sub>2</sub> studies using various experimental systems, complex feedbacks and interactions in natural ecosystems make comprehensive generalizations difficult, especially for old-growth tropical forest ecosystems.

FACE technology (Allen *et al.* 1992) alleviates some of the problems associated with other methods for experimentally increasing ambient CO<sub>2</sub> concentration. Although FACE experiments have been conducted for numerous types of ecosystem, forest FACE studies are quite limited, including those conducted at a loblolly pine (*Pinus taeda*) plantation forest in North Carolina (DeLucia *et al.* 1999; Oren *et al.* 2001; Hamilton *et al.* 2002) and a sweetgum plantation in Tennessee (Norby *et al.* 2001b;

Edwards *et al.* 2002). In the loblolly pine plantation, DeLucia *et al.* (1999) found that NPP was stimulated by ca. 25%, and that this increased productivity was maintained for at least 4 years (Hamilton *et al.* 2002). By contrast, in an adjacent longer-running non-replicated FACE experiment, Oren *et al.* (2001) found that although the growth enhancement was similar to that found in the replicated experiment for the first 3 years (DeLucia *et al.* 1999; Hamilton *et al.* 2002), productivity during years 4–7 returned to rates found in the control plots. Short-term and long-term responses to elevated CO<sub>2</sub> are, in many cases, likely to differ substantially (Luo & Reynolds 1999; McMurtrie *et al.* 2000; Thornley & Cannell 2000) underscoring the need for a cautious approach to broad extrapolations from short-term studies (Oren *et al.* 2001).

There is usually a direct reduction in stomatal conductance in response to elevated CO<sub>2</sub> resulting in increased WUE, and in some cases increased WUE delays the arrival of water stress. Thus, even if photosynthetic rates are not altered under elevated CO<sub>2</sub>, an increase in WUE may reduce water stress and allow greater opportunities for growth (Hättenschwiler *et al.* 1997; Amthor 1999). A delay in water stress may be particularly important in tropical forests. Silva *et al.* (2002) demonstrated that wood tissue production, and hence NPP, is significantly reduced in the dry season in a central Amazon forest, and many tropical forests experience seasonal rainfall. However, it is important to note that Silva *et al.* (2002) found that tree growth was more highly correlated with average than actual monthly precipitation, suggesting that seasonal phenological changes are more important than actual precipitation (e.g. Wright & Cornejo 1990) in determining changes in woody tissue growth. Thus, seasonal changes in precipitation may alter tissue production rates directly through changes in moisture availability, but phenological patterns of leaf growth, senescence and carbon allocation may be much more resistant to change.

The residence time of carbon in different tissues varies considerably in tropical forests. Leaves and fine roots, for example, are short-lived and decompose relatively quickly, whereas slow growing trees of the central Amazon can live for more than 1000 years (Chambers *et al.* 1998, 2001c), and the trunks and branches of large dead trees can take many decades to decompose (Chambers *et al.* 2000). Thus, productivity gains that primarily increase fast-cycling tissues will have little effect on ecosystem carbon storage, but the partitioning of additional photosynthate to woody tissue production will result in relatively large increases in carbon storage. A possible exception to this could be if significant changes in fine litter quality occurred resulting in a negative feedback to decomposition rates.

Experimental studies on how changes in nutrient availability affect NEP under elevated CO<sub>2</sub> can be misleading because, at most, they address only the first few years of the CO<sub>2</sub> response, before ecosystem carbon and nutrient stocks can change substantially. Unless elevated CO<sub>2</sub> is accompanied by increased nutrient inputs, decreased nutrient losses, or increased partitioning of nutrients to long-lived tissues, decreased nutrient availability in response to increased nutrient storage is essentially unavoidable (Field 1999). Thus, what ultimately limits NPP and carbon storage is the progressive decrease in nutrient availability, not the initial levels.

Growth response to elevated CO<sub>2</sub> also appears to be dependent on interactions among trees (Ceulemans *et al.* 1999). For example, Jach & Ceulemans (1999) found that increased relative growth rates for Scots pine were evident only during the first year, and after the canopy closed no consistent growth response to elevated CO<sub>2</sub> was observed. In addition, *Quercus ilex* growing for 30 years near a CO<sub>2</sub> spring exhibited no growth stimulation after canopy closure (Hättenschwiler *et al.* 1997).

In summary, experimental and theoretical evidence suggests that NPP in forested ecosystems may increase by anywhere from zero to 25% under doubled atmospheric CO<sub>2</sub> (from pre-industrial levels). Further constraining this range for tropical forests is hindered by a lack of appropriate large-scale manipulative studies. However, to at least quantify the maximum long-term response of central Amazon forest to an increase in NPP, Chambers *et al.* (2001a) performed a modelling experiment. Briefly, forest carbon cycling is modelled by simulating recruitment, growth, death and decomposition of individual trees in a plot that varies from 10 to 100 ha. The model was parameterized with, and tested against, extensive field data from the central Amazon, and details are provided in Chambers *et al.* (2004b) and Chambers (1998). Using an earlier version of this model, Chambers *et al.* (2001a) increased woody tissue production linearly by 25% (the maximum experimental response) over an arbitrary 50 year interval, and the corresponding increase in total wood biomass demonstrated a maximum sink capacity of ca. 0.5 Mg C ha<sup>-1</sup> yr<sup>-1</sup> for a central Amazon forest.

We use a modified version of the Chambers *et al.* (2001a) model to perform a more realistic model experiment by linking the increase in NPP to the known and expected rise in atmospheric CO<sub>2</sub> concentration (Neftel *et al.* 1985; Friedli *et al.* 1986; IPCC 2000; Keeling & Whorf 2002), with the NPP response following a so-called beta (β)-function (Amthor & Koch 1996). Model results indicated a remarkably long lag-time before total tree biomass reached a new dynamic equilibrium, and a maximum sink capacity of ca. 0.2 Mg C ha<sup>-1</sup> yr<sup>-1</sup>, which became evident only several decades into the twenty-first century (figure 1). For comparison with carbon accumulation measured on a network of tropical forests inventory plots (ca. 0.5 Mg C ha<sup>-1</sup> yr<sup>-1</sup>; Phillips *et al.* 1998), the model predicted a carbon sink strength for calendar years 1980–2020 of only 0.05 Mg C ha<sup>-1</sup> yr<sup>-1</sup> or approximately one order of magnitude less than Phillips *et al.* (1998). Thus, at least for this central Amazon forest, it appears unlikely that recent changes in biomass dynamics and species composition (Phillips & Gentry 1994; Phillips *et al.* 1998, 2002) are being driven by elevated CO<sub>2</sub>. We suspect that changes in other environmental factors, such as increased forest disturbance during the latter part of the twentieth century (Chambers *et al.* 2004b), the geometry of solar radiation (Farquhar & Roderick 2003; Gu *et al.* 2003) and shifts in mean annual precipitation (Schuur 2003) are more plausible potential drivers of this non-equilibrium behaviour of old-growth tropical forests.

## 6. TREE MORTALITY AND SUCCESSION

Changes in disturbance frequency and tree mortality in tropical forests can have large impacts on forest structure

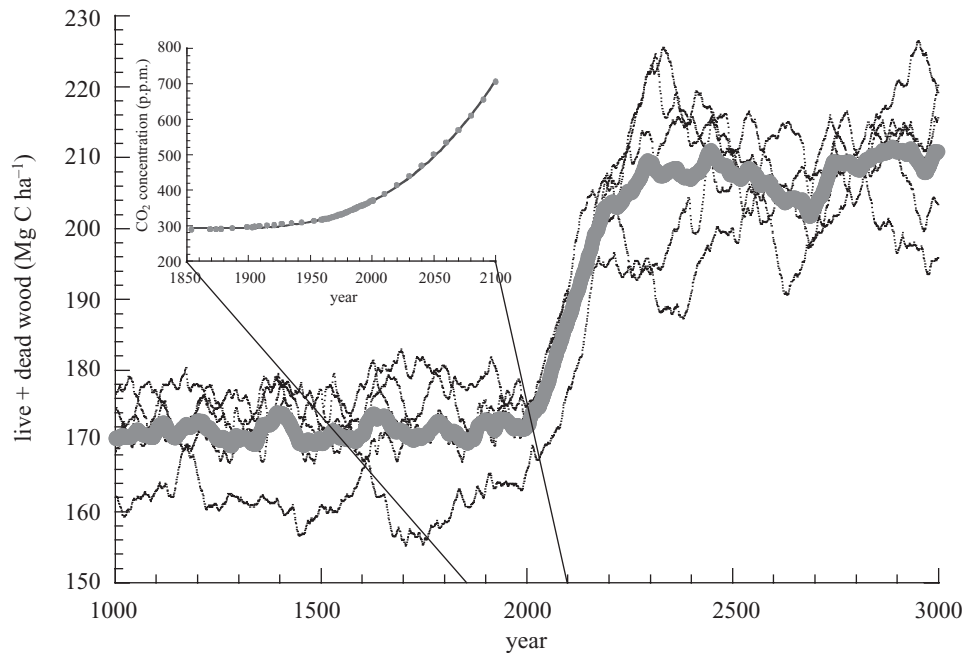


Figure 1. Modelled response of total wood carbon (trees and woody surface litter) in a central Amazon forest to a 25% increase in NPP with five model runs at 10 ha each (thick line, mean response). The increase in NPP was tied to the known and expected increase in atmospheric  $\text{CO}_2$  from 1850 to 2100 (insert graph) using a  $\beta$ -function (see text). Near the year 2200, carbon storage reached a new dynamic equilibrium with a 25% increase. In this model experiment, response was remarkably slow, with an accumulation rate of  $0.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  not evident for several decades into the twenty-first century, and an accumulation rate for the period 1980–2020 of only  $0.05 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ .

and functioning, and there is evidence that changes are occurring in tropical forests. For example, Phillips & Gentry (1994) found that rates of both tree mortality and recruitment have increased since the 1950s, with most of the increase since the 1980s for 22 pantropical old-growth forest sites. Although the cause of this observed increase in forest turnover is unclear, climate change and deforestation are possible sources (Phillips & Gentry 1994). Strong ENSO events have been pronounced during the latter part of the twentieth century (Fedorov & Philander 2000), and the frequency and intensity of ENSO events may be linked to climate change (Timmermann *et al.* 1999). Also, because the presence or absence of vegetation can alter the hydrological cycle and surface energy budget, deforestation can also influence regional climate (Shukla & Mintz 1982; Lawton *et al.* 2001). Shukla *et al.* (1990), for example, estimated that complete deforestation of the Amazon basin would result in a *ca.* 25% reduction in regional precipitation.

Phillips *et al.* (2002) documented an increase in the dominance of woody climbing plants (lianas) in Amazonian forests by using a series of permanent inventory plots. Because lianas thrive in disturbed environments, this change may be partly due to increased forest turnover rates (Phillips & Gentry 1994) that would increase the forest fraction in gap regeneration phase. Although lianas may also respond more favourably to elevated  $\text{CO}_2$  concentration, the present-day increase is probably not yet sufficient to drive noticeable changes (figure 1), although  $\text{CO}_2$ -driven changes in species composition may become increasingly important as atmospheric  $\text{CO}_2$  continues to increase throughout the twenty-first century. Increased disturbance can result in rapid shifts in ecosystem processes and tree species composition (Laurance *et al.* 1997,

1998*a,b*), whereas  $\text{CO}_2$ , increasing at a present rate of *ca.*  $1.7 \text{ p.p.m.v. yr}^{-1}$ , is more likely to cause gradual shifts in forest species composition. Hättenschwiler *et al.* (1997) found that oak tree growth in natural  $\text{CO}_2$  springs was enhanced only during the first 25–30 years of growth, whereas mature trees were not affected by elevated  $\text{CO}_2$ , suggesting that the early regeneration phase may respond more to elevated  $\text{CO}_2$  than mature forests.

In many tropical forests, most gaps are relatively small and the abundance of true pioneer species (e.g. *Cecropia* spp., *Vismia* spp.) is low. For example, gaps smaller than  $200 \text{ m}^2$  were 76% of all canopy openings at La Selva Biological Station (Sanford *et al.* 1986), and daily integrated light levels in these small gaps are less than 20% full sunlight (Denslow *et al.* 1990). Several ecological processes are thought to vary as a function of gap size. The species composition of trees that fill gaps, for example, is often quite similar to that of the surrounding forest, and only once a gap passes a critical large size do pioneer species become abundant (Hubbell *et al.* 1999). The size of gaps may also affect nutrient availability and other factors such as soil temperature and soil moisture (Fetcher *et al.* 1985; Uhl *et al.* 1988; Silver *et al.* 1996; Denslow *et al.* 1998). However, results from Denslow *et al.* (1998) indicate that the vast majority of shade-tolerant species are little affected by gap-induced changes in nutrient availability, and that these changes may mostly favour high-light-demanding species. Thus tree mortality and gap formation typically result in relatively small changes in biogeochemical cycling, although once a critical threshold is passed, forest structure and functioning can change dramatically.

Changing atmospheric conditions may result in synergistic effects that ultimately result in marked changes in the structure and functioning of tropical forests. First,

changes in disturbance frequency, such as ENSO events and the intensity of convective storms, may alter the size and abundance of canopy gaps. Increased tree mortality will not only initiate regeneration in gaps, but will also result in increased growth for mature canopy trees owing to the release of local competition for resources (Chambers *et al.* 2004b). Elevated mortality will be particularly important if the largest trees are impacted more heavily. In many tropical forests a large fraction of the above-ground biomass is stored in a few of the largest trees (Brown *et al.* 1995), and Laurance *et al.* (2000) found that mortality rates for the largest trees increased more than smaller trees in response to forest fragmentation. Elevated atmospheric CO<sub>2</sub> may have little effect on most mature canopy trees (Hättenschwiler *et al.* 1997), but increased carbon availability may give competitive advantages to some species such as light-demanding pioneers, climbing woody plants and trees having mutualistic relationships with nitrogen-fixing organisms.

## 7. NUTRIENT UPTAKE

Nutrient availability is well known to influence plant response to elevated CO<sub>2</sub> (Arnone & Körner 1995; Winter *et al.* 2001a). In temperate ecosystems, low N availability often limits NPP and has the potential to inhibit growth responses to CO<sub>2</sub> fertilization (Finzi *et al.* 2002). In highly weathered soils typical of tropical forests, N is relatively abundant and P is the most commonly limiting element to NPP. This is because P is supplied primarily through the weathering of parent material, whereas N accumulates through biological processes (McGill & Cole 1981). Soil P becomes depleted over long time periods because the gradual leaching of organic and mineral forms are not balanced by replacement from rock weathering, atmospheric inputs or other depositional processes. Phosphorus can also become limiting to vegetation because of P occlusion with Fe and Al oxides and hydroxides, and the formation of resistant secondary minerals. Because highly weathered tropical soils typically have abundant reactive Fe and Al minerals, the removal of P from the rapidly cycling labile pool through these mechanisms is thought to be a dominant fate of P in these ecosystems (Uehara & Gillman 1981).

The question of whether P limitation will inhibit the growth response to elevated CO<sub>2</sub> in tropical forests is complex. Plants have evolved several mechanisms to alleviate low P stress, including associations with mycorrhizal fungi (Went & Stark 1968); the ability to produce enzymes that may help release P adsorbed on exchanged sites or held in organic molecules; the ability to resorb P from foliar tissue before leaf senescence (Vitousek 1984; Silver 1994); and a strategy of allocating significant C to root biomass on or near the soil surface to efficiently cycle P from decaying organic matter (Stark & Jordan 1978). The response of these processes to elevated CO<sub>2</sub> is more likely to control nutrient interactions with elevated CO<sub>2</sub> than direct changes in nutrient uptake in tropical forests.

In a recent review, Lloyd *et al.* (2001) suggest that tropical forests are not strongly limited by P, and that P limitation will not inhibit a potential growth response under elevated CO<sub>2</sub>. Their argument stems from two primary assumptions: (i) that the labile P pool is in equilibrium with the non-labile pool over time periods relevant to

current atmospheric changes; and (ii) that P mineralization and uptake in soils will keep pace with P demand due to the production of organic acids associated with root and mycorrhizal activity. The Lloyd *et al.* (2001) proposal that tropical forests are not truly limited by P contradicts widely held beliefs that low P pools strongly influence rates of tropical forest growth.

Long-term fertilization studies have not been conducted in low elevation, old-growth tropical systems, but studies in montane forests on highly weathered soils have shown a significant delay in any increased above-ground growth following fertilizations (Tanner *et al.* 1990, 1992). No studies have explored the possibility of shifts in carbon allocation following fertilization in tropical forests that might contribute to the observed increase in above-ground biomass production. Native vegetation is likely to be adapted to the resource conditions under which it occurs (Chapin 1980); certainly high NPP and the evolution of mechanisms to enhance P acquisition, suggest that these forests are able to access and take up adequate P. However, the assumption that tropical forests could increase their P capture and uptake over a relatively short time periods (associated with current the CO<sub>2</sub> fertilization effect), and sustain this increased growth, is not strongly supported by previous research. First, the labile P pool is unlikely to be in equilibrium with the less labile pools over the time-scale relevant to our ability to detect a CO<sub>2</sub> fertilization effect. Lloyd *et al.* (2001) use the Langmuir model to describe the dynamics of P movement from sorbed to soluble fractions. The migration of PO<sub>4</sub> ions from labile pools to adsorbed and then to occluded pools is likely to occur on the scale of hours to weeks. By contrast, the diffusion of P from sorbed or Fe and Al bound forms, occurs on a scale of many decades or longer (Tinker & Nye 2000). Thus, an increase in P demand due to CO<sub>2</sub> fertilization may result in the depletion of the labile pool with a much slower rate of replacement than assumed by Lloyd *et al.* (2001).

Factors controlling rates of P mineralization are not well understood in tropical forests. For rates of P mineralization to increase commensurately with an increase in growth rates under elevated CO<sub>2</sub>, stimulation of microbial activity and/or the production of phosphatase enzymes are required. A study using a cultivated wheat species found that root phosphatase production increased under elevated CO<sub>2</sub> when soil P levels were low (Barrett *et al.* 1998). We know of no similar studies on tropical forest tree species, and too little is known about the behaviour of phosphatase production in tropical forests, to predict the response to elevated CO<sub>2</sub>. There is good evidence that the mycorrhizal associations can be maintained under elevated CO<sub>2</sub>, and as Lloyd *et al.* (2001) point out, this is likely to result from more root tissue available for infection than from direct CO<sub>2</sub> enhancement.

In summary, there is not yet sufficient evidence to discount the possibility that nutrients and specifically P will limit the ability of tropical forests to enhance growth under elevated CO<sub>2</sub>. While we agree with Lloyd *et al.* (2001) that tropical forests have evolved numerous strategies to help offset the strong P sorption capacity of highly weathered tropical forest soils, mechanisms to increase P acquisition sufficiently to lead to a measurable growth response lack experimental evidence.

## 8. FINE AND COARSE LITTER DYNAMICS AND SOIL ORGANIC MATTER STORAGE

Because NEP is the difference between NPP and heterotrophic respiration, factors that change either process result in changes in ecosystem carbon storage. However, most research focuses on the input side of this equation, and much less work has been performed on respiration of SOM and dead plant material. Both production and decomposition are likely to be directly or indirectly sensitive to atmospheric changes in CO<sub>2</sub> levels, temperature and precipitation. These processes and their degree of coupling are also likely to be affected by the frequency and severity of disturbance events. Litterfall is thought to be balanced by decomposition over short periods of one or more years, but few studies have measured this directly. If atmospheric change has a greater proportional impact on one of the two processes, then significant positive or negative feedbacks in carbon cycling may occur. For example, if trees are more drought tolerant than heterotrophs, then drying events could increase standing stocks on the forest floor and lead to changes in soil temperature, moisture and potentially increase the probability of fire. It is generally assumed that the flux of nutrients and carbon from decomposing litter provides the bulk of nutrients for plant growth over short time periods (*sensu* Stark & Jordan 1978). It follows that forests are likely to rapidly equilibrate to new steady-state conditions of litter production and decomposition with climate change owing to nutrient limitation. Again, this has never been tested and may underestimate the importance of the soil and SOM as reservoirs of labile nutrients (Tiessen *et al.* 1994).

There has been considerable work done to estimate rates of fine litter production in tropical forests (Clark *et al.* 2001), and rates vary strongly with precipitation (Silver 1998). Above-ground fine-litter production ranges from 0.8 Mg C ha<sup>-1</sup> yr<sup>-1</sup> ( $n = 37$ ) in seasonally dry tropical forests to 8 Mg C ha<sup>-1</sup> yr<sup>-1</sup> ( $n = 93$ ) in humid tropical forests. Similarly, litterfall appears to be sensitive to temperature in the tropics, although the relationships are often not linear. Much less work has been done to relate decomposition to climate and climate change in the tropics. Litter decomposition rates often correlate with litter quality when climate and edaphic conditions are held constant. Some studies have found changes in litter quality and quantity under elevated CO<sub>2</sub> (Norby *et al.* 2001a; Hamilton *et al.* 2002) and inferred changes in decay rates (Melillo *et al.* 1993). However, when tropical plants were grown under elevated CO<sub>2</sub> conditions, litter quality and decay rates were unchanged (Hirschel *et al.* 1997). Few studies have looked at the effects of temperature on decomposition in the tropics. Litterfall decomposition rates often decrease exponentially with increasing elevation in the tropics suggesting an effect of temperature, although rates appear to be most sensitive to litterfall N concentrations (Silver 1998).

Tropical forests growing on highly weathered soils often allocate considerable photosynthate to root biomass (Jackson *et al.* 1996). Roots are more buffered against climate changes than above-ground tissues by their location in the soil. Fine root production rates (less than 2 mm diameter) range from 0.6 to 7.7 Mg C ha<sup>-1</sup> yr<sup>-1</sup> in tropical forests, and follow no apparent biome-level trend with

precipitation or temperature (Silver 1998). Fine root decomposition rates range from 0.3 to 0.9 yr<sup>-1</sup> (Silver & Miya 2001) and turnover ranges from 0.04 to 2.6 yr<sup>-1</sup> (Gill & Jackson 2000). In mesocosm studies, tropical plants increased their allocation to roots when exposed to elevated CO<sub>2</sub> and high soil nutrient conditions (Körner & Arnone 1992), but under low nutrient availability there was no statistically significant increase in root biomass with CO<sub>2</sub> fertilization (Arnone & Körner 1995). Controls over the rate of coarse litter decomposition (trunks and branches greater than 10 cm in diameter) are also poorly understood, although work in the central Amazon has demonstrated that decomposition rates vary with wood density, diameter and moisture content and that the respiratory flux from coarse litter was similar in magnitude to that from fine litter (Chambers *et al.* 2000, 2001b).

The largest changes in litter dynamics under elevated CO<sub>2</sub> conditions will probably be linked to alterations in litter production, either from increased productivity or changes in disturbance frequency. For example, at the Duke FACE site, Hamilton *et al.* (2002) found a 165% increase in total heterotrophic respiration in response to elevated CO<sub>2</sub> (+ 200 p.p.m.v.), largely brought about by an increase in litter production. Thus, if much of any additional productivity under elevated CO<sub>2</sub> is allocated to fast-cycling tissues or exudates, forest carbon balance may be little changed.

Another potentially important C sink in tropical forests is SOM. Tropical forests store approximately the same amount of C below ground as above ground (Brown *et al.* 1993; Dixon *et al.* 1994). Soil C storage occurs through four primary mechanisms: free particulate organic matter, C sorption to mineral surfaces (Christensen 1992), C–C associations, generally through hydrophobic bonding (Piccolo & Mbagwu 1999) and C storage in soil aggregates (Oades & Waters 1991). These processes can be related when, for example, aggregation is enhanced through mineral and hydrophobic associations. In general, C stored in stable aggregates and associated with mineral surfaces is thought to have longer turnover times than free SOM and C–C bonds although this has not been thoroughly examined in tropical forests.

The deep profiles and fine texture of many tropical forest soils, together with the high proportion of amorphous organic and mineral material result in very large soil C storage capacity. The rate of deposition may or may not be balanced by heterotrophic respiration. The mean residence time for surface soil C in tropical forests is generally relatively short (6–30 years; Townsend *et al.* 1995; Trumbore *et al.* 1995), but can be very long when SOM reacts with certain amorphous minerals such as allophane, common in young volcanic soils (Torn *et al.* 1997). Deep highly weathered tropical soils may be especially important repositories for C. Carbon inputs from deep roots found in seasonally dry tropical forests can dramatically increase the soil C pools at depth, which tend to have a very slow turnover time (less than 1000 years) when compared with surface soil environments (Trumbore *et al.* 1995).

Detecting changes in soil C pools with elevated CO<sub>2</sub>, climate change and associated environmental changes can be very difficult in tropical forests owing to the large soil C pool size, although stable and radioisotope techniques are dramatically increasing our ability to identify changes

in soil C pools and fluxes. The factors that are most likely to lead to greater soil C storage in mature tropical forests are: (i) increased hydrophobicity of litter through changes in plant species composition or litter quality; (ii) increased rooting depth associated with decreased soil moisture or nutrient availability; (iii) increased C allocation to root biomass and root exudates both of which can affect the amount of C inputs and mean residence times; and (iv) greater root density and fungal associations that contribute to the formation of stable aggregates. Any one or combination of these factors could contribute to greater soil C storage over relatively short time periods. However, although many tropical soils clearly have a large long-term carbon storage capacity, Telles *et al.* (2003) demonstrate that the annual sink capacity is relatively low, and not likely to be important over annual to decadal time-scales.

## 9. SUMMARY

Elevated CO<sub>2</sub> (doubled pre-industrial) studies in natural ecosystems have demonstrated NPP increases of 0–25%, with plants growing under nutrient stress showing the lowest response. Because many tropical forests occur on nutrient-deficient soils, evidence to support a 25% increase in NPP for many tropical forests under elevated CO<sub>2</sub> is non-existent. In addition, evolutionary constraints of plants adapted to low CO<sub>2</sub> levels during much of the Late Pleistocene, may limit tree response to additional carbon. However, to at least constrain the maximum expected carbon sequestration response for a central Amazon forest, we performed a model experiment with a 25% increase in NPP (using a  $\beta$ -function) tied to the known and expected rise in CO<sub>2</sub> concentration from 1850 to 2100 (figure 1). The low sequestration rate predicted by the model (0.2 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) is not only considerably less than measured in a global network of forest inventory plots (Phillips *et al.* 1998), but because of a significant lag time, sequestration due to an assumed CO<sub>2</sub> fertilization response would only become evident well into the twenty-first century. We suspect that changes being observed in tropical forests (Phillips & Gentry 1994; Phillips *et al.* 1998, 2002) are more plausibly being driven by changes in other environmental factors, such as disturbance (Chambers *et al.* 2004b) or solar radiation (Gu *et al.* 2003), which have the capacity to cause more rapid shifts in ecosystem carbon storage than increasing atmospheric CO<sub>2</sub>. An important area to focus research effort is distinguishing among processes that result in short-term transient shifts in ecosystem carbon balance, from those that have the potential to cause long-term relatively permanent changes.

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## REFERENCES

- Allen Jr, L. H., Drake, B. G., Rogers, H. H. & Shinn, J. H. 1992 Field techniques for exposure of plants and ecosystems to elevated carbon dioxide and other trace gases. *Crit. Rev. Pl. Sci.* **11**, 85–119.
- Amthor, J. S. 1995 Predicting effects of atmospheric CO<sub>2</sub> partial pressure on forest photosynthesis. *Global Ecol. Biogeogr. Lett.* **22**, 243–274.
- Amthor, J. S. 1997 Plant respiratory responses to elevated carbon dioxide partial pressure. In *Advances in carbon dioxide effects research* (ed. L. H. Allen Jr, M. B. Kirkham, D. M. Olszyk & C. E. Whitman), pp. 35–77. Madison, WI: American Society of Agronomy.
- Amthor, J. S. 1999 Increasing atmospheric CO<sub>2</sub> concentration, water use, and water stress: scaling up from the plant to the landscape. In *Carbon dioxide and environmental stress* (ed. Y. Luo & H. A. Mooney), pp. 33–55. San Diego, CA: Academic Press.
- Amthor, J. S. 2000 Direct effect of elevated CO<sub>2</sub> on nocturnal *in situ* leaf respiration in nine temperate deciduous tree species is small. *Tree Physiol.* **20**, 139–144.
- Amthor, J. S. & Koch, G. W. 1996 Biota growth factor b: stimulation of terrestrial ecosystem net primary production by elevated atmospheric CO<sub>2</sub>. In *Carbon dioxide and terrestrial ecosystems* (ed. G. W. Koch & H. A. Mooney), pp. 399–414. San Diego, CA: Academic Press.
- Amthor, J. S., Koch, G. W., Willms, J. R. & Layzell, D. B. 2001 Leaf O<sub>2</sub> uptake in the dark is independent of coincident CO<sub>2</sub> partial pressure. *J. Exp. Bot.* **52**, 2235–2238.
- Arnone, J. A. I. & Körner, C. 1995 Soil and biomass carbon pools in model communities of tropical plants under elevated CO<sub>2</sub>. *Oecologia (Berlin)* **104**, 61–71.
- Barrett, D. J., Richardson, A. E. & Gifford, R. M. 1998 Elevated atmospheric CO<sub>2</sub> concentrations increase wheat root phosphatase activity when growth is limited by phosphorus. *Aust. J. Pl. Physiol.* **25**, 87–93.
- Bazzaz, F. A. 1990 The response of natural ecosystems to the rising global CO<sub>2</sub> levels. *A. Rev. Ecol. Syst.* **21**, 167–196.
- Beerling, D. J., Heath, J., Woodward, F. I. & Mansfield, T. A. 1996 Drought–CO<sub>2</sub> interactions in trees—observations and mechanisms. *New Phytol.* **134**, 235–242.
- Beerling, D. J., Osborne, C. P. & Chaloner, W. G. 2001 Do drought-hardened plants suffer from fever? Response. *Trends Pl. Sci.* **6**, 507–508.
- Berry, J. A. & Björkman, O. 1980 Photosynthetic response and adaptation to temperature in higher plants. *A. Rev. Pl. Physiol.* **31**, 491–543.
- Bloom, A. J., Chapin, F. S. I. & Mooney, H. A. 1985 Resource limitation in plants—an economic analogy. *A. Rev. Ecol. Syst.* **16**, 363–392.
- Brown, I. F., Martinelli, L. A., Thomas, W. W., Moreira, M. Z., Ferreira, C. A. C. & Victoria, R. A. 1995 Uncertainty in the biomass of Amazonian forests: an example from Rondônia, Brazil. *Forest Ecol. Mngmt* **75**, 175–189.
- Brown, S., Hall, C. A. S., Knabe, W., Raich, J., M.C., T. & Woerner, P. 1993 Tropical forests: their past, present and potential future role in the terrestrial carbon budget. *Water, Air Soil Pollut.* **70**, 357–371.
- Bruhn, D., Mikkelsen, T. N. & Atkin, O. K. 2002 Does the direct effect of atmospheric CO<sub>2</sub> concentration on leaf respiration vary with temperature? Responses in two species of *Plantago* that differ in relative growth rate. *Physiol. Plantarum* **114**, 57–64.
- Bunce, J. A. 2001 Effects of prolonged darkness on the sensitivity of leaf respiration to carbon dioxide concentration in C<sub>3</sub> and C<sub>4</sub> species. *Ann. Bot. Lond.* **87**, 463–468.
- Carey, E. V., Delucia, E. H. & Ball, J. T. 1996 Stem maintenance and construction respiration in *Pinus ponderosa* grown in different concentrations of atmospheric CO<sub>2</sub>. *Tree Physiol.* **16**, 125–130.
- Ceulemans, R., Janssens, I. A. & Jach, M. E. 1999 Effects of CO<sub>2</sub> enrichment on trees and forests: lessons to be learned in view of future ecosystem studies. *Ann. Bot.* **84**, 577–590.

- Chambers, J. Q. 1998 The role of large wood in the carbon cycle of Central Amazon rain forest. PhD thesis, University of California, Santa Barbara, CA, USA.
- Chambers, J. Q., Higuchi, N. & Schimel, J. P. 1998 Ancient trees in Amazonia. *Nature* **391**, 135–136.
- Chambers, J. Q., Higuchi, N., Ferreira, L. V., Melack, J. M. & Schimel, J. P. 2000 Decomposition and carbon cycling of dead trees in tropical forests of the Central Amazon. *Oecologia* **122**, 380–388.
- Chambers, J. Q., Higuchi, N., Tribuzy, E. S. & Trumbore, S. E. 2001a Carbon sink for a century. *Nature* **410**, 429.
- Chambers, J. Q., Schimel, J. P. & Nobre, A. D. 2001b Respiration from coarse wood litter in Central Amazon forests. *Biogeochemistry* **52**, 115–131.
- Chambers, J. Q., Van Eldik, T., Southon, J. & Higuchi, N. 2001c Tree age structure in tropical forests of Central Amazonia. In *Lessons from Amazonia* (ed. R. O. J. Bierregaard, C. Gascon, T. E. Lovejoy & R. C. G. Mesquita), pp. 68–78. New Haven, CT: Yale University Press.
- Chambers, J. Q., Tribuzy, E. S., Toledo, L. C., Crispim, B. F., Higuchi, N., dos Santos, J., Araújo, A. C., Kruijt, B., Nobre, A. D. & Trumbore, S. E. 2004a Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecol. Appl.* (In the press.)
- Chambers, J. Q., Higuchi, N., Teixeira, L. M., Santos, J. d., Laurance, S. G. & Trumbore, S. E. 2004b Response of tree biomass and wood litter to disturbance in a Central Amazon forest. *Oecologia* (Submitted.)
- Chapin, F. S. I. 1980 The mineral nutrition of wild plants. *A. Rev. Ecol. Syst.* **21**, 423–447.
- Chen, J. Y., Carlson, B. E. & Del Genio, A. D. 2002 Evidence for strengthening of the tropical general circulation in the 1990s. *Science* **295**, 838–841.
- Christensen, B. T. 1992 Physical fractionation of soil organic matter in primary particle size and density separates. *Adv. Soil Sci.* **20**, 1–90.
- Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., Ni, J. & Holland, E. A. 2001 NPP in tropical forests: an evaluation and synthesis of the existing field data. *Ecol. Applic.* **11**, 371–384.
- Condit, R., Hubbell, S. P. & Foster, R. B. 1995 Mortality rates of 205 neotropical tree and shrub species and the impact of severe drought. *Ecol. Monogr.* **65**, 419–439.
- Curtis, P. S. & Wang, X. 1998 A meta-analysis of elevated CO<sub>2</sub> effects on woody plant mass, form, and physiology. *Oecologia* **113**, 299–313.
- Dale, V. H. (and 13 others) 2001 Climate change and forest disturbances. *BioScience* **51**, 723–734.
- DeLucia, E. H. (and 10 others) 1999 Net primary production of a forest ecosystem with experimental CO<sub>2</sub> enrichment. *Science* **284**, 1177–1179.
- Denslow, J. S., Schulz, J. C., Vitousek, P. M. & Strain, B. R. 1990 Growth response of tropical tree shrubs to treefall gap environment. *Ecology* **71**, 165–179.
- Denslow, J. S., Ellison, A. M. & Sanford, R. E. 1998 Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *J. Ecol.* **86**, 597–609.
- de Souza, E. B., Kayano, M. T., Tota, J., Pezzi, L., Fisch, G. & Nobre, C. 2000 On the influence of the El Niño, La Niña and Atlantic dipole pattern on the Amazonian rainfall during 1960–1998. *Acta Amazonica* **30**, 305–318.
- Dixon, R. K., Brown, S., Houghton, R. A., Solomon, A. M., Trexler, M. C. & Wisnieski, J. 1994 Carbon pools and flux of global forest ecosystems. *Science* **263**, 185–190.
- Edwards, N. T., Tschaplinski, T. J. & Norby, R. J. 2002 Stem respiration increases in CO<sub>2</sub>-enriched sweetgum trees. *New Phytol.* **155**, 239–248.
- Ehleringer, J. R. & Field, C. B. (eds) 1993 *Scaling physiological processes leaf to globe*. San Diego, CA: Academic Press.
- Ehret, D. L. & Jolliffe, P. A. 1985 Leaf injury to bean plants grown in carbon dioxide enriched atmospheres. *Can. J. Bot.* **63**, 2015–2020.
- Emanuel, K. 1987 The dependence of hurricane intensity on climate. *Nature* **326**, 483–485.
- Enquist, C. A. F. 2002 Predicted regional impacts of climate change on the geographical distribution and diversity of tropical forests in Costa Rica. *J. Biogeogr.* **29**, 519–534.
- Farquhar, G. D. & Roderick, M. L. 2003 Pinatubo, diffuse light, and the carbon cycle. *Science* **5615**, 1997–1998.
- Farquhar, G. D. & von Caemmerer, S. 1982 Modeling of photosynthetic response to environmental conditions. In *Encyclopedia of plant physiology*, vol. 12B (ed. O. L. Lange, P. S. Nobel & C. B. Osmond), pp. 549–587. Berlin: Springer.
- Farquhar, G. D., von Caemmerer, S. & Berry, J. A. 1980 A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* **149**, 78–90.
- Fearnside, P. M. 1997 Greenhouse gases from deforestation in Brazilian Amazonia: net committed emissions. *Climat. Change* **35**, 321–360.
- Fearnside, P. M. & Barbosa, R. I. 1998 Soil carbon changes from conversion of forest to pasture in Brazilian Amazonia. *Forest Ecol. Mngmt* **108**, 147–166.
- Fedorov, A. V. & Philander, S. G. 2000 Is El Niño changing? *Science* **288**, 1997–2002.
- Fetcher, N., Oberbauer, S. F. & Strain, B. R. 1985 Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *Int. J. Biometeorol.* **29**, 145–155.
- Field, C. B. 1999 Diverse controls on carbon storage under elevated CO<sub>2</sub>: toward a synthesis. In *Carbon dioxide and environmental stress* (ed. Y. Luo & H. A. Mooney), pp. 389–408. San Diego, CA: Academic Press.
- Field, C. B., Jackson, R. B. & Mooney, H. A. 1995 Stomatal responses to increased CO<sub>2</sub>—implications from the plant to the global scale. *Pl. Cell Environ.* **18**, 1214–1225.
- Finzi, A. C., DeLucia, E. H., Hamilton, J. G., Richter, D. D. & Schlesinger, W. H. 2002 The nitrogen budget of a pine forest under free air CO<sub>2</sub> enrichment. *Oecologia* **132**, 567–578.
- Friedli, H., Lotscher, H., Oeschger, H., Siegenthaler, U. & Stauffer, B. 1986 Ice core record of the <sup>13</sup>C/<sup>12</sup>C ratio of atmospheric CO<sub>2</sub> in the past two centuries. *Nature* **324**, 237–238.
- Gifford, R. M. & Evans, L. T. 1981 Photosynthesis, carbon partitioning and yield. *A. Rev. Pl. Physiol.* **32**, 485–509.
- Gill, R. A. & Jackson, R. B. 2000 Global patterns of root turnover for terrestrial ecosystems. *New Phytol.* **147**, 13–31.
- Gonzalez-Meler, M. A. & Siedow, J. N. 1999 Direct inhibition of mitochondrial respiratory enzymes by elevated CO<sub>2</sub>: does it matter at the tissue or whole-plant level? *Tree Physiol.* **19**, 253–259.
- Gonzalez-Meler, M. A., Ribascarbo, M., Siedow, J. N. & Drake, B. G. 1996 Direct inhibition of plant mitochondrial respiration by elevated CO<sub>2</sub>. *Pl. Physiol.* **112**, 1349–1355.
- Gonzalez-Meler, M. A., Giles, L., Thomas, R. B. & Siedow, J. N. 2001 Metabolic regulation of leaf respiration and alternative pathway activity in response to phosphate supply. *Pl. Cell Environ.* **24**, 205–215.
- Grace, J. (and 11 others) 1995 Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992–1993. *Science* **270**, 778–780.
- 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 Biol.* **2**, 209–217.
- Gray, W. M. 1990 Strong association between west African rainfall and United States landfall of intense hurricanes. *Science* **249**, 1251–1256.

- Grime, J. P. 1988 The C–S–R model of primary plant strategies—origins, implications and tests. In *Plant evolutionary biology* (ed. L. D. Gottlieb & S. K. Jain), pp. 371–393. London: Chapman & Hall.
- Gu, L., Baldocchi, D. D., Wofsy, S. C., Munger, J. W., Michalsky, J. J., Urbanski, S. P. & Boden, T. A. 2003 Response of a deciduous forest to the Mount Pinatubo eruption: enhanced photosynthesis. *Science* **299**, 2035–2038.
- Hamilton, J. G., Thomas, R. B. & Delucia, E. H. 2001 Direct and indirect effects of elevated CO<sub>2</sub> on leaf respiration in a forest ecosystem. *Pl. Cell Environ.* **24**, 975–982.
- Hamilton, J. G., DeLucia, E. H., George, K., Naidu, S. L., Finzi, A. C. & Schlesinger, W. H. 2002 Forest carbon balance under elevated CO<sub>2</sub>. *Oecologia* **131**, 250–260.
- Hansen, J. E., Sato, M., Laci, A., Ruedy, R., Tegen, I. & Matthews, E. 1998 Climate forcings in the Industrial era. *Proc. Natl Acad. Sci. USA* **95**, 12 753–12 758.
- Hartmann, D. L. 2002 Climate change—tropical surprises. *Science* **295**, 811–812.
- Hättenschwiler, S., Miglietta, F., Raschi, A. & Korner, C. 1997 Thirty years of *in situ* tree growth under elevated CO<sub>2</sub>: a model for future forest responses? *Global Change Biol.* **3**, 463–471.
- Herold, A. 1980 Regulation of photosynthesis by sink activity: the missing link. *New Phytol.* **99**, 499–507.
- Hirschel, G., Korner, C. & Arnone, J. A. 1997 Will rising atmospheric CO<sub>2</sub> affect leaf litter quality and *in situ* decomposition rates in native plant communities? *Oecologia (Berlin)* **110**, 387–392.
- Holmgren, M., Scheffer, M., Ezcurra, E., Gutierrez, J. R. & Mohren, G. M. J. 2001 El Niño effects on the dynamics of terrestrial ecosystems. *Trends Ecol. Evol.* **16**, 89–94.
- Houghton, R. A. 1991 Tropical deforestation and atmospheric carbon dioxide. *Climat. Change* **19**, 99–118.
- Houghton, R. A., Skole, D. L., Nobre, C. A., Hackler, J. L., Lawrence, K. T. & Chomentowski, W. H. 2000 Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature* **403**, 301–304.
- Hsiao, T. C. & Jackson, R. B. 1999 Interactive effects of water stress and elevated CO<sub>2</sub> on growth, photosynthesis, and water use efficiency. In *Carbon dioxide and environmental stress* (ed. Y. Luo & H. A. Mooney), pp. 3–26. San Diego, CA: Academic Press.
- Hubbell, S. P., Foster, R. B., O'Brien, S. T., Harms, K. E., Condit, R., Wechsler, B., Wright, S. J. & de Lao, S. L. 1999 Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* **283**, 554–557.
- IPCC 2000 Emissions scenarios: summary for policymakers: WMO/UNEP.
- IPCC 2001a *Climate change 2001: impacts, adaptation, and vulnerability: contribution of Working Group II to the third assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.
- IPCC 2001b *Climate change 2001: the scientific basis: contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.
- Ishida, A., Toma, T. & Marjenah 1999 Limitation of leaf carbon gain by stomatal and photochemical processes in the top canopy of *Macaranga conifera*, a tropical pioneer tree. *Tree Physiol.* **19**, 467–473.
- Jach, M. E. & Ceulemans, R. 1999 Effects of elevated atmospheric CO<sub>2</sub> on phenology, growth and crown structure of Scots pine (*Pinus sylvestris*) seedlings after two years of exposure in the field. *Tree Physiol.* **19**, 289–300.
- Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E. & Schulze, E. D. 1996 A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**, 389–411.
- Jahnke, S. & Krewitt, M. 2002 Atmospheric CO<sub>2</sub> concentration may directly affect leaf respiration measurement in tobacco, but not respiration itself. *Pl. Cell Environ.* **25**, 641–651.
- Janous, D., Pokorný, R., Brossaud, J. & Marek, M. V. 2000 Long-term effects of elevated CO<sub>2</sub> on woody tissues respiration of Norway spruce studied in open-top chambers. *Biol. Plantarum* **43**, 41–46.
- Jarvis, P. G. & McNaughton, K. G. 1986 Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* **15**, 1–49.
- Keeling, C. D. & Whorf, T. P. 2002 Atmospheric CO<sub>2</sub> records from sites in the SIO air sampling network. In *Trends: a compendium of data on global change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, TN, U.S.A.
- Kirschbaum, M. U. F. (and 10 others) 1994 Modelling forest response to increasing CO<sub>2</sub> concentration under nutrient-limited conditions. *Pl. Cell Environ.* **17**, 1081–1099.
- Kitajima, K., Mulkey, S. S. & Wright, S. J. 1997 Seasonal leaf phenotypes in the canopy of a tropical dry forest: photosynthetic characteristics and associated traits. *Oecologia (Berlin)* **109**, 490–498.
- Kitao, M., Lei, T. T., Koike, T., Tobita, H., Maruyama, Y., Matsumoto, Y. & Ang, L.-H. 2000 Temperature response and photoinhibition investigated by chlorophyll fluorescence measurements for four distinct species of dipterocarp trees. *Physiol. Plantarum* **109**, 284–290.
- Koch, G. W. & Mooney, H. A. 1996 Response of terrestrial ecosystems to elevated CO<sub>2</sub>: a synthesis and summary. In *Carbon dioxide and terrestrial ecosystems* (ed. G. W. Koch & H. A. Mooney), pp. 415–431. San Diego, CA: Academic Press.
- 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 Physiol.* **14**, 347–360.
- Körner, C. & Arnone III, J. A. 1992 Responses to elevated carbon dioxide in artificial tropical ecosystems. *Science* **257**, 1672–1675.
- Lambers, H. 1982 Cyanide-resistant respiration: a non-phosphorylating electron transport pathway acting as an energy overflow. *Physiol. Plantarum* **55**, 478–485.
- Lambers, H. 1997 Respiration and the alternative oxidase. In *A molecular approach to primary metabolism in plants* (ed. C. H. Foyer & P. Quick), pp. 295–309. London: Taylor & Francis.
- Lambers, H., Chapin, F. S. I. & Pons, T. L. 1998 *Plant physiological ecology*. New York: Springer.
- Laurance, W. F., Laurance, S. G., Ferreira, L. V., Rankin-de Merona, J. M., Gascon, C. & Lovejoy, T. E. 1997 Biomass collapse in Amazonian forest fragments. *Science* **278**, 1117–1118.
- Laurance, W. F., Ferreira, L. V., Rankin-de Merona & Laurance, S. G. 1998a Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* **6**, 2032–2040.
- Laurance, W. F., Laurance, S. G. & Delamonica, P. 1998b Tropical forest fragmentation and greenhouse gas emissions. *Forest Ecol. Mngmt* **110**, 173–180.
- Laurance, W. F., Delamonica, P., Laurance, S. G., Vasconcelos, H. L. & Lovejoy, T. E. 2000 Conservation—rainforest fragmentation kills big trees. *Nature* **404**, 836.
- Lawton, R. O., Nair, U. S., Pielke, R. A. & Welch, R. M. 2001 Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science* **294**, 584–587.
- Lloyd, J. & Farquhar, G. D. 1996 The CO<sub>2</sub> dependence of photosynthesis, plant growth responses to elevated atmospheric CO<sub>2</sub> concentrations and their interaction with soil nutrient status. 1. General principles and forest ecosystems. *Funct. Ecol.* **10**, 4–32.

- Lloyd, J., Bird, M. I., Veenendaal, E. M. & Kruijff, B. 2001 Should phosphorus availability be constraining moist tropical forest responses to increasing CO<sub>2</sub> concentrations? In *Global biogeochemical cycles in the climate system* (ed. E. D. Schulze), pp. 95–114. San Diego, CA: Academic Press.
- Lugo, A. E. & Scatena, F. N. 1996 Background and catastrophic tree mortality in tropical moist, wet and rain forests. *Biotropica* **28**, 585–599.
- Luo, Y. Q. & Reynolds, J. F. 1999 Validity of extrapolating field CO<sub>2</sub> experiments to predict carbon sequestration in natural ecosystems. *Ecology* **80**, 1568–1583.
- McGill, W. B. & Cole, C. V. 1981 Comparative aspects of cycling of organic C, N, S and P through soil organic matter. *Geoderma* **26**, 267–286.
- McMurtrie, R. E., Dewar, R. C., Medlyn, B. E. & Jeffreys, M. P. 2000 Effects of elevated (CO<sub>2</sub>) on forest growth and carbon storage: a modelling analysis of the consequences of changes in litter quality/quantity and root exudation. *Pl. Soil* **224**, 135–152.
- Marshall, J. D. & Monserud, R. A. 1996 Homeostatic gas-exchange parameters inferred from C-13/C-12 in tree rings of conifers. *Oecologia* **105**, 13–21.
- Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore III, B., Vorosmarty, C. J. & Schloss, A. L. 1993 Global climate change and terrestrial net primary productivity. *Nature* **363**, 234–240.
- Mooney, H. A. & Chiariello, N. R. 1984 The study of plant function—the plant as a balanced system. In *Perspectives on plant population ecology* (ed. R. Dirzo & J. Sarukhan), pp. 305–323. Sunderland, MA: Sinauer.
- Mora, G. & Pratt, L. M. 2001 Isotopic evidence for cooler and drier conditions in the tropical Andes during the last glacial stage. *Geology* **29**, 519–522.
- Mulkey, S. S., Smith, A. P., Wright, S. J., Machado, J. L. & Dudley, R. 1992 Contrasting leaf phenotypes control seasonal variation in water loss in a tropical forest shrub. *Proc. Natl Acad. Sci. USA* **89**, 9084–9088.
- Nefel, A., Moor, E., Oeschger, H. & Stauffer, B. 1985 Evidence from polar ice cores for the increase in atmospheric CO<sub>2</sub> in the past two centuries. *Nature* **315**, 45–47.
- Nelson, B. W., Kapos, V., Adams, J. B., Oliveira, W. J., Braun, O. P. G. & do Amaral, I. L. 1994 Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology* **75**, 853–858.
- Ng, C. K. Y. & Hew, C. S. 1999 Regulation of photosynthesis by end-product accumulation in leaves of the C<sub>3</sub> tropical epiphytic orchid hybrid, *Oncidium Goldiana*. *Lindleyana* **14**, 2–11.
- Norby, R. J., Wullschleger, S. D., Gunderson, C. A., Johnson, D. W. & Ceulemans, R. 1999 Tree responses to rising CO<sub>2</sub> in field experiments: implications for the future forest. *Pl. Cell Environ.* **22**, 683–714.
- Norby, R. J., Cotrufo, M. F., Ineson, P., O'Neill, E. G. & Canadell, J. G. 2001a Elevated CO<sub>2</sub>, litter chemistry, and decomposition: a synthesis. *Oecologia* **127**, 153–165.
- Norby, R. J., Todd, D. E., Fulps, J. & Johnson, D. W. 2001b Allometric determination of tree growth in a CO<sub>2</sub>-enriched sweetgum stand. *New Phytol.* **150**, 477–487.
- Oades, J. M. & Waters, A. G. 1991 Aggregate hierarchy in soils. *Australian J. Soil Res.* **29**, 815–828.
- Oberbauer, S. F., Strain, B. R. & Fetcher, N. 1985 Effect of carbon dioxide enrichment on seedling physiology and growth of two tropical tree species. *Physiol. Plantarum* **65**, 352–356.
- Oren, R. (and 10 others) 2001 Soil fertility limits carbon sequestration by forest ecosystems in a CO<sub>2</sub>-enriched atmosphere. *Nature* **411**, 469–472.
- Peterson, A. G. (and 12 others) 1999 The photosynthesis leaf nitrogen relationship at ambient and elevated atmospheric carbon dioxide: a meta-analysis. *Global Change Biol.* **5**, 331–346.
- Petit, J. R. (and 18 others) 1999 Climate and atmospheric history of the past 420 000 years from the Vostok ice core, Antarctica. *Nature* **399**, 429–436.
- Phillips, O. L. & Gentry, A. H. 1994 Increasing turnover through time in tropical forests. *Science* **263**, 954–958.
- Phillips, O. L. (and 10 others) 1998 Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* **282**, 439–442.
- Phillips, O. L. (and 17 others) 2002 Increasing dominance of large lianas in Amazonian forests. *Nature* **418**, 770–774.
- Piccolo, A. & Mbagwu, J. S. C. 1999 Role of hydrophobic components of soil organic matter in soil aggregate stability. *Soil Sci. Soc. Am. J.* **63**, 1801–1810.
- Poorter, H. & Perez-Soba, M. 2001 The growth response of plants to elevated CO<sub>2</sub> under non-optimal environmental conditions. *Oecologia* **129**, 1–20.
- Reekie, E. G. & Bazzaz, F. A. 1989 Competition and patterns of resource use among seedlings of five tropical trees grown at ambient and elevated carbon dioxide. *Oecologia (Berlin)* **79**, 212–222.
- Reich, P. B. 1995 Phenology of tropical forests—patterns, causes, and consequences. *Can. J. Bot.* **73**, 164–174.
- Rogers, A. & Ellsworth, D. S. 2002 Photosynthetic acclimation of *Pinus taeda* (loblolly pine) to long-term growth in elevated pCO<sub>2</sub> (FACE). *Pl. Cell Environ.* **25**, 851–858.
- Ronchail, J., Cochonneau, G., Molinier, M., Guyot, J. L., Chaves, A. G. D., Guimaraes, V. & de Oliveira, E. 2002 Interannual rainfall variability in the Amazon basin and sea-surface temperatures in the equatorial Pacific and the tropical Atlantic Oceans. *Int. J. Climatol.* **22**, 1663–1686.
- Sage, R. F. 1995 Was low atmospheric CO<sub>2</sub> during the Pleistocene a limiting factor for the origin of agriculture? *Global Change Biol.* **1**, 93–106.
- Sage, R. F. & Coleman, J. R. 2001 Effects of low atmospheric CO<sub>2</sub> on plants: more than a thing of the past. *Trends Pl. Sci.* **6**, 18–24.
- Sage, R. F. & Cowling, S. A. 1999 Implications of stress in low CO<sub>2</sub> atmospheres of the past: are today's plants too conservative for a high CO<sub>2</sub> world. In *Carbon dioxide and environmental stress* (ed. Y. Luo & H. A. Mooney), pp. 289–304. San Diego, CA: Academic Press.
- Sanchez, P. A. 1976 *Properties and management of soils in the tropics*. New York: Wiley.
- Sanford Jr, R. L., Braker, H. E. & Hartshorn, G. S. 1986 Canopy openings in a primary neotropical lowland forest. *J. Trop. Ecol.* **2**, 277–282.
- Schuur, E. A. G. 2003 Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation. *Ecology* **84**, 1165–1170.
- Shukla, J. & Mintz, Y. 1982 Influence of land-surface evapotranspiration on the Earth's climate. *Science* **215**, 1498–1501.
- Shukla, J., Nobre, C. & Sellers, P. 1990 Amazon deforestation and climate change. *Science* **247**, 1322–1325.
- Silva, R. P., Santos, J., Tribuzy, E. S., Chambers, J. Q., Nakamura, S. & Higuchi, N. 2002 Diameter increment and growth patterns for individual trees in Central Amazon, Brazil. *Forest Ecol. Mngmt* **116**, 295–301.
- Silver, W. L. 1994 Is nutrient availability related to plant nutrient use in humid tropical forests. *Oecologia* **98**, 336–343.
- Silver, W. L. 1998 The potential effects of elevated CO<sub>2</sub> and climate change on tropical forests soils and biogeochemical cycling. *Climat. Change* **39**, 337–361.
- Silver, W. L. & Miya, R. K. 2001 Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia (Berlin)* **129**, 407–419.
- Silver, W. L., Brown, S. & Lugo, A. E. 1996 Effects of changes in biodiversity on ecosystem function in tropical forests. *Conserv. Biol.* **10**, 17–24.

- Stark, N. M. & Jordan, C. F. 1978 Nutrient retention by the root mat of an Amazonian rain forest. *Ecology* **59**, 434–437.
- Stitt, M. 1991 Rising carbon dioxide levels and their potential significance for carbon flow in photosynthetic cells. *Pl. Cell Environ.* **14**, 741–762.
- Stitt, M. 1994 Flux control at the level of the pathway: studies with mutants and transgenic plants having a decreased activity of enzymes involved in photosynthesis partitioning. In *Flux control in biological systems: from enzymes to populations and ecosystems* (ed. E. D. Schulze), pp. 13–36. San Diego, CA: Academic Press.
- Stitt, M. & Schulze, E. D. 1994 Plant growth, storage, and resource allocation: from flux control in a metabolic chain to whole-plant level. In *Flux control in biological systems: from enzymes to populations and ecosystems* (ed. E. D. Schulze), pp. 57–118. San Diego, CA: Academic Press.
- Tanner, E. V. J., Kapos, V. & Franco, W. 1992 Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. *Ecology* **73**, 78–86.
- Tanner, E. V. J., Kapos, V., Freskos, S., R., H. J. & Theobald, A. M. 1990 Nitrogen and phosphorus fertilization of Jamaican montane forest trees. *J. Ecol.* **6**, 231–238.
- Telles, E. C. C., Camargo, P. B., Martinelli, L. A., Trumbore, S. E., Costa, E. S., Santos, J., Higuchi, N. & Oliveira, R. O. 2003 Influence of soil texture on carbon dynamics and storage potential in tropical soils of Amazonia. *Global Biogeochem. Cycles* **17**, 1040.
- Thomas, R. B. & Strain, B. R. 1991 Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. *Pl. Physiol.* **96**, 627–634.
- Thornley, J. H. M. & Cannell, M. G. R. 2000 Modelling the components of plant respiration: representation and realism. *Ann. Bot.* **85**, 55–67.
- Tiessen, H., Cuevas, E. & Chacon, P. 1994 The role of soil organic matter in sustaining soil fertility. *Nature* **371**, 783–785.
- Tilman, D. 1993 Carbon dioxide limitation and potential direct effects of its accumulation on plant communities. In *Biotic interactions and global change* (ed. P. M. Kareiva, J. G. Kingsolver & R. B. Huey), pp. 333–346. Sunderland, MA: Sinauer.
- Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M. & Roeckner, E. 1999 Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* **398**, 694–697.
- Tinker, P. B. & Nye, P. H. 2000 *Solute movement in the rhizosphere*. Topics in sustainable agronomy. New York: Oxford University Press.
- Tjoelker, M. G., Oleksyn, J. & Reich, P. B. 1999 Acclimation of respiration to temperature and CO<sub>2</sub> in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biol.* **5**, 679–691.
- Tjoelker, M. G., Oleksyn, J., Lee, T. D. & Reich, P. B. 2001 Direct inhibition of leaf dark respiration by elevated CO<sub>2</sub> is minor in 12 grassland species. *New Phytol.* **150**, 419–424.
- Tognetti, R., Cherubini, P. & Innes, J. L. 2000 Comparative stem-growth rates of Mediterranean trees under background and naturally enhanced ambient CO<sub>2</sub> concentrations. *New Phytol.* **146**, 59–74.
- Torn, M. S., Trumbore, S. E., Chadwick, O. A., Vitousek, P. M. & Hendricks, D. M. 1997 Mineral control of soil organic carbon storage and turnover. *Nature* **389**, 170–173.
- Townsend, A. R., Vitousek, P. M. & Trumbore, S. E. 1995 Soil organic-matter dynamics along gradients in temperature and land-use on the island of Hawaii. *Ecology* **76**, 721–733.
- Trumbore, S. E., Davidson, E. A., Barbosa de Carmago, P., Nepstad, D. C. & Martinelli, L. A. 1995 Belowground cycling of carbon in forests and pastures of Eastern Amazonia. *Global Biogeochem. Cycles* **9**, 515–528.
- Uehara, G. & Gillman, G. P. 1981 *The mineralogy, chemistry, and physics of tropical soils with variable charge clays*. Westview tropical agriculture series; no. 4. Boulder, CO: Westview Press.
- Uhl, C., Clark, K., Dezzio, N. & Maquirino, P. 1988 Vegetation dynamics in Amazonian treefall gaps. *Ecology* **69**, 751–763.
- Vanderhammen, T. & Absy, M. L. 1994 Amazonia during the last glacial. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **109**, 247–261.
- Vitousek, P. M. 1984 Litterfall, nutrient cycling and nutrient limitation in tropical forests. *Ecology* **65**, 285–298.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395.
- Went, F. W. & Stark, N. M. 1968 Mycorrhiza. *BioScience* **18**, 1035.
- Wielicki, B. A. (and 12 others) 2002 Evidence for large decadal variability in the tropical mean radiative energy budget. *Science* **295**, 841–844.
- Williams, M., Malhi, Y., Nobre, A. D., Rastetter, E. B., Grace, J. & Pereira, M. G. 1998 Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: a modelling analysis. *Pl. Cell Environ.* **21**, 953–968.
- Williamson, G. B., Laurance, W. F., Oliveira, A. A., Delamonica, P., Gascon, C., Lovejoy, T. E. & Pohl, L. 2000 Amazonian tree mortality during the 1997 El Niño drought. *Conserv. Biol.* **14**, 1538–1542.
- Winter, K., Garcia, M., Lovelock, C. E., Gottsberger, R. & Popp, M. 2000 Responses of model communities of two tropical tree species to elevated atmospheric CO<sub>2</sub>: growth on unfertilized soil. *Flora* **195**, 289–302.
- Winter, K., Aranda, J., Garcia, M., Virgo, A. & Paton, S. R. 2001a Effect of elevated CO<sub>2</sub> and soil fertilization on whole-plant growth and water use in seedlings of a tropical pioneer tree, *Ficus insipida* Willd. *Flora* **196**, 458–464.
- Winter, K., Garcia, M., Gottsberger, R. & Popp, M. 2001b Marked growth response of communities of two tropical tree species to elevated CO<sub>2</sub> when soil nutrient limitation is removed. *Flora* **196**, 47–58.
- Wright, S. J. 1996 Phenological responses to seasonality in tropical forest plants. In *Tropical forest plant ecophysiology* (ed. S. S. Mulkey, R. L. Chazdon & A. P. Smith), pp. 440–460. New York: Chapman & Hall.
- Wright, S. J. & Cornejo, F. D. 1990 Seasonal drought and leaf fall in a tropical forest. *Ecology* **71**, 1165–1175.
- Wright, S. J. & Van Schaik, C. P. 1994 Light and the phenology of tropical trees. *Am. Nat.* **143**, 192–199.
- Würth, M. K. R., Winter, K. & Korner, C. 1998 *In situ* responses to elevated CO<sub>2</sub> in tropical forest understorey plants. *Funct. Ecol.* **12**, 886–895.
- Ziska, L. H., Hogan, K. P., Smith, A. P. & Drake, B. G. 1991 Growth and photosynthetic response of nine tropical species with long-term exposure to elevated carbon dioxide. *Oecologia* **86**, 383–389.

## GLOSSARY

- ENSO: El Niño Southern Oscillation  
 FACE: free air CO<sub>2</sub> enrichment  
 LAI: leaf area index  
 NEP: net ecosystem productivity  
 NPP: net primary production  
 Rubisco: ribulose-bisphosphate carboxylase-oxygenase  
 SOM: soil organic matter  
 WUE: water use efficiency