

Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition

Deborah A. Clark*

Department of Biology, University of Missouri–St Louis, St Louis, MO 63121, USA

How tropical rainforests are responding to the ongoing global changes in atmospheric composition and climate is little studied and poorly understood. Although rising atmospheric carbon dioxide (CO₂) could enhance forest productivity, increased temperatures and drought are likely to diminish it. The limited field data have produced conflicting views of the net impacts of these changes so far. One set of studies has seemed to point to enhanced carbon uptake; however, questions have arisen about these findings, and recent experiments with tropical forest trees indicate carbon saturation of canopy leaves and no biomass increase under enhanced CO₂. Other field observations indicate decreased forest productivity and increased tree mortality in recent years of peak temperatures and drought (strong El Niño episodes). To determine current climatic responses of forests around the world tropics will require careful annual monitoring of ecosystem performance in representative forests. To develop the necessary process-level understanding of these responses will require intensified experimentation at the whole-tree and stand levels. Finally, a more complete understanding of tropical rainforest carbon cycling is needed for determining whether these ecosystems are carbon sinks or sources now, and how this status might change during the next century.

Keywords: climate change; atmospheric carbon dioxide; tropical rainforests; photosynthesis; respiration; temperature

1. INTRODUCTION

Tropical rainforests play a major role in the global carbon budget. They have been estimated to account for 32–36% of terrestrial NPP (Melillo *et al.* 1993; Field *et al.* 1998). The large and rapid ongoing changes in atmospheric CO₂ concentration and climate are likely to significantly affect carbon cycling in this biome. This is a global as well as a regional concern, because even small shifts in the ratio between photosynthesis and respiration in these forests can greatly affect the rate of accumulation of atmospheric CO₂ (Clark *et al.* 2003). The integrated effect of changing atmospheric CO₂ concentration and climatic factors on the carbon balance of tropical rainforests is currently unknown. There are few data from this biome that can be used to assess the responses of mature trees or whole stands to these changing factors. There have been no forest-level experiments to test the response of old-growth tropical forest to changes in either CO₂ concentration or temperature (however, stand-level drydown experiments in the Amazon to test for the effects of increasing drought are providing evidence of large impacts (Nepstad *et al.*

2002)). Even more fundamental, for no tropical forest has there been a field assessment of total ecosystem carbon storage and the change in that storage over time.

Multiple studies over the past several years have suggested that tropical rainforests are a significant global carbon sink, possibly in response to the increase in atmospheric CO₂ concentration. At the same time, other lines of evidence raise the possibility that rising temperatures and increasing drought severity will make tropical rainforests an increasing net carbon source to the atmosphere. Determining the current net carbon balance of these ecosystems and how this balance is likely to change is an urgent research need for projecting the rate of atmospheric CO₂ accumulation, and thus climate change, in the coming decades.

In this essay, I review the evidence so far about the responses of tropical rainforests (defined here as lowland tropical moist and tropical wet forests) to atmospheric CO₂ concentrations and climatic factors. I then discuss the implications of these findings with respect to trends in the carbon balance of old-growth stands in this biome. I conclude with a research agenda for resolving the great uncertainty about the current and future carbon balance of the world's tropical forests.

2. ONGOING ATMOSPHERIC AND CLIMATIC CHANGES

For several thousand years preceding the Industrial Revolution, atmospheric CO₂ concentration was

*Addresses for correspondence: (for express mail only) Organizacion para Estudios Tropicales (OET), 450mts al Oeste del Colegio Lincoln, Moravia Frente a Servicentro Los Colegios, San Jose, Costa Rica and (regular mail) INTERLINK-341, POB 02-5635, Miami, FL 33102, USA (daclark@sloth.ots.ac.cr).

One contribution of 17 to a Theme Issue 'Tropical forests and global atmospheric change'.

280 ± 10 p.p.m. Over the past 250 years, CO₂ levels have risen at rates unprecedented during at least the past 20 000 years, to 367 p.p.m. by 1999 (Prentice *et al.* 2001). A 32% increase over pre-industrial levels, the current CO₂ concentration is higher than has existed at any time during the past 420 000 years (Petit *et al.* 1999).

The recent increases in atmospheric concentrations of CO₂ and of other anthropogenic greenhouse gases have been paralleled by rising temperatures. Over the past century the net change in global mean surface temperature was 0.6 ± 0.2 °C (Folland *et al.* 2001). Minimum temperatures are rising faster than maximum temperatures, thus decreasing the daily temperature range (Easterling *et al.* 1997). In the instrumental record maintained since 1861, the 1990s were the warmest decade and 1998 was the warmest year; these are also likely to be peak values for the last millennium (Folland *et al.* 2001). Although the temperature increases have varied spatially, with the most rapid rise at high latitudes, significant warming has occurred throughout the tropics (Folland *et al.* 2001). Since the mid-1970s, the temperature increases in tropical forest regions are estimated to have averaged 0.26 °C per decade (Malhi & Wright 2004).

Over the past two decades, mean surface temperatures and precipitation for the global tropical land region have been generally anticorrelated; thus, years of temperature peaks for the tropics as a whole have also usually been years of anomalously low rainfall averaged over the region (Keeling & Piper 2001; Los *et al.* 2001). However, because long-term rainfall trends vary strongly within the tropics (Malhi & Wright 2004), the relationship between rainfall and temperature varies among sites. In the more seasonal forests across the tropics, the very strong El Niño events of 1982/1983 and 1997/1998 brought both record-high temperatures and record-low rainfall (Leighton & Wirawan 1986; Leigh *et al.* 1990; Hammond & ter Steege 1998; Harrison 2001; Laurance & Williamson 2001). In wetter, less seasonal forests, however (e.g. La Selva, Costa Rica; OTS, unpublished data), the peak temperatures in such strong El Niño events have occurred without decreased rainfall.

A big unknown is whether photosynthetically active radiation has been changing in either total amount or quality for tropical rainforests. There is some evidence from ground stations that global incoming solar radiation has declined over the past 50 years owing to increased aerosols and/or cloud cover (Roderick & Farquhar 2002). The very limited ground monitoring of total incoming radiation and its diffuse fraction in tropical forest regions makes it difficult to determine the existence of any such trends, or to quantify the short-term changes in irradiance during events such as the 1997/1998 mega-Niño. Although data from one satellite have been interpreted as indicating that the tropics experienced a large increase in incoming solar radiation between the 1980s and the 1990s (Chen *et al.* 2002; Wielicki *et al.* 2002; Nemani *et al.* 2003), there are significant uncertainties about this dataset, and it is so far unsupported by other satellite or ground data (Trenberth 2002). There is also a complex interplay between forest productivity, total incoming solar radiation and the diffuse fraction. An increased proportion of diffuse light has been linked to greater efficiency of forest carbon uptake, and increased aerosols and/or cloud

cover have raised the diffuse fraction of incoming light in many world regions (Roderick *et al.* 2001; Gu *et al.* 2003). In addition to any long-term trends, there could be large inter-year variation in this aspect of solar radiation in the tropics. The peak in aerosols from the massive fires in both the Amazon (Laurance & Williamson 2001) and Indonesia (Harrison 2001; Siegert *et al.* 2001; Thompson *et al.* 2001; Page *et al.* 2002) during the 1997/1998 mega-Niño event must have affected the quantity and quality of incoming solar irradiance for large expanses of tropical forest.

When considering the potential effects of increasing atmospheric CO₂ and climatic changes on tropical forests, we need to take into account the differences in temporal variability and scales of change shown by these factors. For example, during the 1980s, atmospheric CO₂ concentration increased at the rate of 1.6 p.p.m. per year (Prentice *et al.* 2001); annual increases varied during that decade, but the range in these net gains per year (Keeling *et al.* 2001) was very small when expressed as a proportion of total atmospheric CO₂ (ca. 0.3–0.7% yr⁻¹). By contrast, site-based measurements of temperature and rainfall showed notable interannual changes during the same decade (between-year increases of 1.4–3.0 °C in weekly maximum temperatures of two dry season months between 1982 and 1983, and a four week extension of the rainless period in 1983, Barro Colorado Island, Panama (Leigh *et al.* 1990), a 1.1 °C difference between consecutive annual means of daily minimum temperature, 1985/1986 versus 1986/1987, La Selva, Costa Rica, OTS unpublished records). Observations of forest responses to such interannual climatic changes over decades-long time-series provide one indication of these ecosystems' potential responses to climatic shifts over the longer term, although such projections must be tentative owing to the possibility of shifting responses owing to acclimation or substrate limitation. Also, short-term extreme events can have large lasting impacts on tropical forest function and composition (e.g. through selective mortality of large trees or trees of given families or functional types) and could therefore play an important role in the forests' response over future decades.

There is a high probability that both atmospheric CO₂ and global mean temperatures will continue increasing substantially during this century (Albritton *et al.* 2001). Expected greenhouse gas emissions (and a current lack of technology to mitigate them (Hoffert *et al.* 2002)) make it virtually certain that atmospheric CO₂ concentrations will exceed 450 p.p.m. by 2100 (Albritton *et al.* 2001; O'Neill & Oppenheimer 2002). A very much higher concentration could occur by that time if there is a decreasing sink strength in terrestrial ecosystems, as has been projected by some coupled climate–vegetation models (e.g. 980 p.p.m. (Cox *et al.* 2000) and 790 p.p.m. (White *et al.* 2000)). For the Amazon, southeast Asian tropics and African tropics, a recent climate simulation projected additional surface warming of 2.9, 2.1 and 2.5 °C, respectively, if atmospheric CO₂ concentrations rise to 660 p.p.m. (Zhang *et al.* 2001). Another simulation (Bounoua *et al.* 1999) projected a similar temperature increase (2.5 °C) for tropical forests as a whole at 700 p.p.m. atmospheric CO₂. One coupled climate–vegetation simulation projected temperature increases of

more than 4.5 °C for some tropical land areas by 2100 (White *et al.* 2000). Based on recent climate history, it is to be expected that the continued warming will involve large short-term temperature excursions above the prevailing mean, rather than proceeding linearly over time (see White *et al.* 2000). Such excursions will bring higher temperatures earlier than indicated by the smoothed projected trends based on increasing greenhouse gas concentrations. As noted above, increased drought is likely to accompany this warming in the more seasonal parts of the tropics. In the past two decades, the extreme years in terms of tropical temperatures and drought have occurred in very strong El Niño events. Although the interaction between the ENSO cycle and climate change is still imperfectly understood (Fedorov & Philander 2000), one strong possibility is that the continued warming will amplify ENSO, increasing both the frequency and the severity of El Niño events (Cole 2001). These changes could also be accompanied by significant changes in incoming solar irradiance and its diffuse fraction.

3. IMPACTS OF ATMOSPHERIC AND CLIMATIC CHANGES ON TROPICAL FORESTS

(a) *A suite of contrasting changes*

As outlined above, tropical rainforests have been experiencing rapid climatic and atmospheric changes over the past 250 years, and the pace of these changes is likely to continue or accelerate through the current century. The functioning of these forests will continue to involve an integrated response to all these changes, some of which may be promoting increased productivity or increased total carbon storage and some of which may be promoting decreased productivity or carbon storage, with nonlinear interactions among them highly likely as well (Rowland-Bamford 2000). Although direct monitoring of temporal trends in tropical forest function is clearly critically needed, additional kinds of research will be required for realistic projections of future forest performance. As recently emphasized by Field (2001), we need a process-level understanding of forest-level responses to the changing climatic and atmospheric factors, singly and in combination. This is beyond our current reach for tropical rainforests, given the scanty relevant data for the biome. As noted in recent reviews (Körner 1995a, 1998, 2001; Arnone 1996), artificial conditions and a focus on young life stages in most elevated CO₂ experiments with tropical rainforest plants greatly restrict the usefulness of the findings for projecting whole-forest responses. Some recent experiments, however, have used more realistic environmental conditions and have explicitly focused on model communities or mature forest trees. There are also several studies that bear on the potential responses of tropical forest plants to changes in temperature, drought and other factors. A review of this work provides a useful starting point for assessing the likely relative impacts of climatic and atmospheric changes on the performance of tropical forest trees and stands.

(b) *Responses to increased atmospheric carbon dioxide concentrations*

There have been a handful of experimental studies of the effects of CO₂ enrichment on tropical forest plants

growing in otherwise natural conditions (exposed to ambient climate, rooted in natural soil and in competition with other plants). In two studies canopy tree leaves were accessed from a canopy crane in a tropical dry forest in Panama and exposed to doubled CO₂. Lovelock *et al.* (1999) measured leaf- and branchlet-level responses over 40 weeks for one canopy tree species. Although photosynthetic rates increased *ca.* 30% with elevated CO₂, no increase was detected in biomass production (foliage or reproductive structures). There was, however, a 20% increase in branchlet concentrations of TNCs, suggesting local carbon saturation. Even stronger TNC increases (+41% to +61%) were found in leaves by Würth *et al.* (1998a) when they exposed *in situ* canopy leaves of four other tree species to doubled CO₂. In a third such 'natural-conditions' CO₂ study (Würth *et al.* 1998b), seedlings of five local species (a grass, two trees and two shrubs) were planted in the understorey of a Panamanian closed forest. For 15 months, half of the seedlings were maintained at doubled CO₂ and half at ambient CO₂. After a seven month to 1 year delay, all species showed significant increases in seedling growth with enhanced CO₂, but the response decreased with increasing understorey light levels, and it also varied strongly among species. As in the canopy-level studies, leaf TNC levels increased under enhanced CO₂ for two of the species.

In only one experiment so far have model 'communities' of tropical rainforest trees been outplanted in natural substrate and exposed to elevated CO₂. Lovelock *et al.* (1998) grew assemblages of 10 tropical forest tree species at ambient and doubled CO₂ in open-top chambers at a forest edge in Panama. During the six months of the experiment, the plants grew from *ca.* 20 cm tall seedlings to 2 m tall saplings. The elevated CO₂ levels produced no enhancement in biomass accumulation. Observed effects of the high CO₂ included reductions in leaf area index, increased leaf starch concentrations, increases in leaf carbon:nitrogen ratios and increased photosynthetic rates. Although the different species responded individually, the 'late-successional' species tended to respond less to the elevated CO₂ than did the pioneer and 'mid-successional' species.

Arnone (1996) reviewed the elevated-CO₂ experiments conducted with model communities of tropical plants in growth chambers. The four experiments varied in initial plant size (from small seedlings to 30–70 cm tall saplings), duration (21–530 days) and soil fertility. In none of the four experiments did elevated CO₂ result in a significant change in biomass accumulation or in leaf area index. All these experiments produced a significant shift in community composition in the high-CO₂ treatment.

Finally, Rosenthal (1998) estimated total carbon exchange of a tropical rainforest plant assemblage (age *ca.* 6–8 years) in a 0.17 hectare (ha, where 1 ha = 10⁴ m²) mesocosm at Biosphere II, at the very high and diurnally varying 'ambient' CO₂ levels of the mesocosm (average *ca.* 900 p.p.m.), and after a two week period at lower CO₂ (average *ca.* 450 p.p.m.). During a few daily cycles of measurement, estimated net daytime carbon uptake was significantly greater at the higher CO₂ level; night-time respiration did not differ between CO₂ levels. As the author notes, however, the measurements were over a short time-span, and several aspects of the system (e.g.

Arizona soil with a pH of more than 7; the very large within-day swings in CO₂ concentration, atypical light regime, air flushing to depress CO₂ levels) are highly unnatural.

Clearly, more and longer-term experiments are needed to probe the potential effects of increasing atmospheric CO₂ on tropical rainforests. One consistent response in the experiments so far, however, has been a marked increase in TNCs either in leaves or twigs, with a resulting increase in carbon : nitrogen ratios; such decreased tissue quality could have far-reaching consequences for nutrient cycling, herbivory and other forest processes (Ceulemans *et al.* 1999). The second consistent finding from *in situ* branches on mature forest trees and from young tree assemblages has been a lack of enhancement in either biomass production or leaf area index, with doubled CO₂. These results contrast strongly with the increased growth and leaf area seen in numerous elevated-CO₂ experiments on individually potted plants. As has been emphasized by others (Arnone 1996; Körner 1998), several features of such experiments make them ill-suited for scaling up to the forest level: restriction to very small plants, the atypically high availability of water and nutrients, growth in the absence of plant competition and the lack of other real-world processes such as herbivory and pathogen pressure. The more realistic experiments so far, although without question biased by their relatively short duration, have suggested that tropical rainforests at elevated CO₂ levels will show a decrease in tissue quality and little or no enhancement of biomass production rates.

(c) *Increasing temperature*

There have not yet been any experiments on mature tropical forest trees or with model communities of tropical forest plants to assess the effects of warming on tree and forest function. Several lines of evidence, however, suggest that these forests, already at relatively high temperatures, might be among the first vegetation types to show strong negative impacts of increased warming.

Photosynthesis shows a characteristically parabolic response to temperature; above the temperature optimum for a given plant species or ecotype, photosynthesis decreases markedly owing to a combination of factors (Baldocchi & Amthor 2001). Measurements of canopy leaves in a broad range of tropical forests (Oberbauer 1983; Huc & Guehl 1989; Ishida *et al.* 1996; Zotz & Winter 1996; Keller & Lerdau 1999; Lerdau & Throop 1999; Graham *et al.* 2003) have documented sharp declines in photosynthetic rates at leaf temperatures above 26–34 °C (e.g. figure 1a). Such temperatures are already being experienced by canopy leaves in these forests. Canopy leaf temperatures in tropical forests can be 1–7 °C above air temperature (Koch *et al.* 1994; Grace *et al.* 1996a; Ishida *et al.* 1996; Zotz & Winter 1996). During the 1997/1998 El Niño, air temperatures at a Costa Rican tropical wet forest site, La Selva, reached 30–36 °C on 73% of the days (OTS, unpublished records). Even in less extreme years, tropical canopy trees have been frequently found to show a depression in photosynthesis around midday, at times of high temperatures and high vapour pressure deficits (Oberbauer 1983; Koch *et al.* 1994; Zotz & Winter 1996).

With global warming, leaf temperatures will continue to rise. Based on the observations reviewed above, it is likely

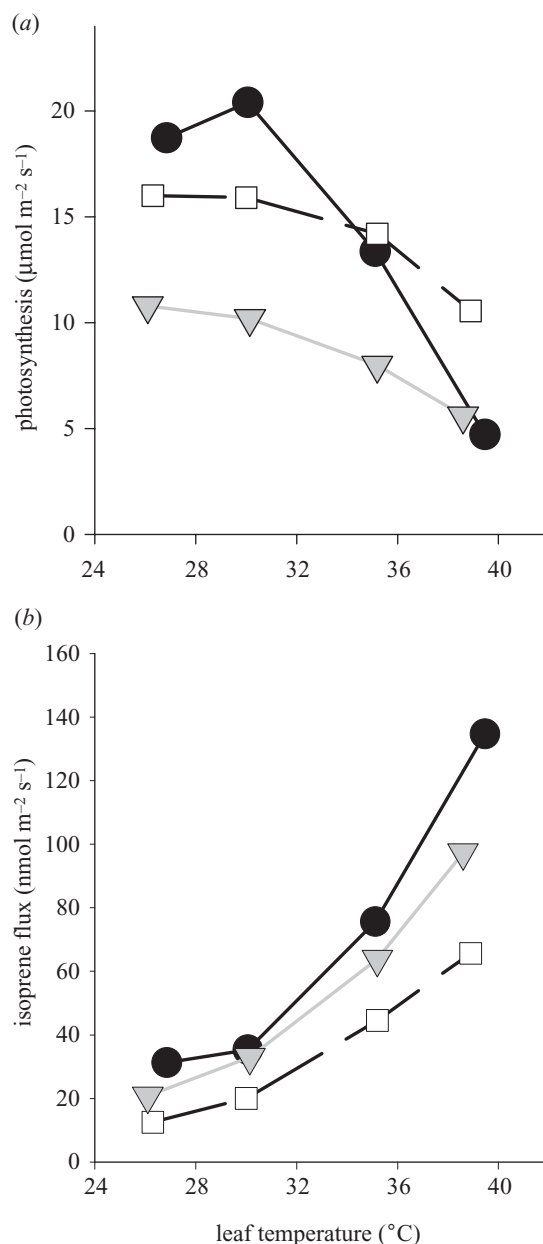


Figure 1. The strong temperature responses of (a) net photosynthesis and (b) isoprene emission by canopy leaves of three tropical dry forest species, Parque Metropolitan, Panama (measured from the canopy crane, at constant humidity). Canopy trees: black circles, *Ficus insipida* (Moraceae); white squares, *Luehea seemannii* (Malvaceae). Liana: grey triangles, *Stigmaphyllon hypargyreum* (Malpighiaceae). (Redrawn from Keller & Lerdau (1999), with permission.)

that the not-so-distant future will bring periods when canopy leaf temperatures in tropical lowland forests reach levels where the photosynthetic apparatus is damaged (40–55 °C (Fitter & Hay 1981; Baldocchi & Amthor 2001)); such damage can occur after exposures as brief as 30 min (Fitter & Hay 1981). Meanwhile, the frequency of daytime periods when leaf temperatures exceed 26–34 °C is likely to have been generally increasing in these forests through recent years, and it will certainly increase in coming decades. Current photosynthetic responses of tropical forest plants suggest that daytime carbon uptake is significantly decreased at such temperatures. Any decrease in

stomatal conductance with increasing CO₂ levels could further raise leaf temperatures and such an effect would have particularly strong effects on those species already near their thermal limits (Bazzaz 1998).

Another fundamental process is respiration. Autotrophic respiration (R_a) has a very different short-term temperature response from that of photosynthesis: as temperature increases, R_a increases exponentially. While ecosystem-level estimation of total plant respiration in forests involves large uncertainties owing to methods issues, it is clear that R_a plays a large role in forest carbon budgets; in tropical forests, it is likely to be at least 50–60% of GPP (Amthor & Baldocchi 2001). Ryan *et al.* (1994a) measured bole respiration of two canopy tree species in a Costa Rican tropical wet forest and found the Q_{10} (the proportional increase with a 10 °C temperature increase) to be 2.1, indicating that bole respiration rates increase 8% and 24% with temperature rises of 1 and 3 °C, respectively. Q_{10} values for respiration by foliage, twigs and coarse roots are generally higher than those for bole respiration (Ryan *et al.* 1994b).

NPP, the ‘gasoline’ that runs forest function, is the difference between total forest photosynthesis and plant respiration (GPP – R_a). The combined effect of photosynthetic and respiration responses to temperature could be strongly decreasing tropical forest NPP with rising temperatures. The net CO₂ exchange (emission or uptake) by tropical forests, NEE, could be similarly affected. NEE is the difference between NPP and heterotrophic respiration (R_h). R_h , although not measured directly for any forest because of major methods issues, also appears to increase exponentially with increasing temperature in both temperate and tropical ecosystems (Holland *et al.* 2000). Thus, what we currently know about the responses of photosynthesis and both R_a and R_h to temperature suggests that continued warming will bring for tropical forests ongoing declines in the ratio GPP : R_a and a continuing shift in NEE towards increased carbon emission.

The possibility exists, however, that acclimation or substrate limitation will modify the responses of these processes to continued temperature increases (Körner 1995b; Amthor & Baldocchi 2001; Baldocchi & Amthor 2001; Saxe *et al.* 2001). If tropical forest plants or microbes show significant acclimatization of their respiration response, the increase in ecosystem respiration with temperature could be much less than that indicated by short-term measurements (Körner 1995b; Gifford 2003). Similarly, the photosynthetic temperature response has generally been found to be very plastic, varying seasonally and among ecotypes within a species (Baldocchi & Amthor 2001; Saxe *et al.* 2001). Tropical forest trees thus might show significant upward shifts of their photosynthetic temperature optimum.

It has been suggested (Hogan *et al.* 1991), however, that tropical plants, with their relatively constricted ambient temperature ranges compared with those of temperate plants, might be particularly ill-equipped to adjust to ever higher temperatures. Bazzaz (1998) has also pointed out that the palaeorecord suggests a higher sensitivity of tropical lowland forests to warming, based on the much stronger floristic shifts seen in these ecosystems than in temperate forests with quite small temperature changes during the Pleistocene. Consistent with these ideas are

findings from experiments comparing the photosynthetic temperature responses of tropical and temperate tree species. In one such study (Read 1990), the photosynthetic responses to temperature were tested for seedlings of the tree genus *Nothofagus*: seven tropical montane species and seven temperate species and ecotypes. Significant shifts were found in the temperature optimum of all taxa when seedlings were maintained for two week periods at different constant-temperature regimes. The tropical species, however, showed narrower tolerances than the temperate species, and the maximum photosynthetic capacity of the two ‘warmest’ tropical species (from 900 m and 1950 m elevation) was strongly depressed (to only 30–42% of the species’ maximum) when the seedlings were acclimatized at the highest experimental temperature, 32 °C. In a similar experiment with seedlings of eight Australian canopy tree species, four from lowland temperate forests and four from lowland tropical forests (Cunningham & Read 2003), the temperate species were able to maintain 80% of their maximum photosynthetic rates over a much larger temperature range than the tropical species.

Another important temperature response is the production of BVOCs by tropical forest trees (Crutzen *et al.* 1999, 2000). These compounds are a component of NPP that forests ‘lose out the top’. Although forest-level data are limited, it has been estimated that tropical forests produce at least 80% of the total global emissions of these compounds (Lerdau *et al.* 1997). For isoprene, one of the major BVOCs, the temperature response of emission by tropical plants has been found to be exponential, with very strong increases occurring at leaf temperatures of 27–40 °C (Harley *et al.* 1999; Keller & Lerdau 1999; Lerdau & Throop 1999; Geron *et al.* 2002; see figure 1b). At high temperatures (above 38 °C), tropical forest canopy leaves can lose 8–25% of the total assimilated carbon as isoprene (Sharkey & Yeh 2001; Geron *et al.* 2002). Surveys in three neotropical forests (Keller & Lerdau 1999; Lerdau & Throop 1999; Geron *et al.* 2002) have found 29–50% of tested plant species to be significant isoprene emitters. The few available data suggest that tropical forests may also be emitting significant amounts of other BVOCs, such as acetone, methanol and methyl chloride (Geron *et al.* 2002; Yokouchi *et al.* 2002).

Taken together, these observations point to the possibility of severe negative effects of ongoing global warming on the productivity and net carbon exchange of tropical forests, owing to the combined effects of several physiological responses of plants and microbes to temperature. Nevertheless, long-term ecosystem-level responses could be unpredictable given that any changes in the quality and quantity of litter inputs above and below ground could have complex potential effects on microbial respiration and on nutrient cycling (Holland *et al.* 2000; Kirschbaum *et al.* 2003).

(d) Increasing drought

For many of the more seasonal tropical regions, years of peak temperatures in recent decades have also been years of anomalously low rainfall. If this trend continues, tropical forests in such areas will be affected by both higher temperatures and increasing drought as warming proceeds. Salafsky (1998) analysed long-term rainfall data for a site in West Kalimantan (Indonesia) and found that

the amount of dry-season rainfall has been decreasing markedly since 1948, both for El Niño years and for the non-Niño years. Given the physiological stresses imposed by drought (see the literature review in Nepstad *et al.* (2002)), such a trend is likely to have large forest-level impacts, including both decreased forest productivity and increased tree mortality. With increased water stress the trees can be expected to increase the length of the midday depression in canopy uptake and to show decreased maximum photosynthetic capacity (Zotz & Winter 1996). Water stress also increases the impact of carbon losses through isoprene emission; isoprene emission rates are relatively unaffected during periods when photosynthesis is reduced by water deficits (Harley *et al.* 1999).

Two large-scale forest droughting experiments are underway in the Brazilian Amazon. Early results from the first of these studies (Nepstad *et al.* 2002) have demonstrated the existence of multiple, accumulating effects on forest function from enhanced drought; among the early responses were a strong decrease in the above-ground biomass increment of subcanopy trees, canopy thinning and decreased photosynthetic capacity for some tree species. One valuable aspect of such experiments is that they separate effects of increased water limitation from those of higher temperatures, something that will not be possible with observational studies because of the co-occurrence of these factors in the more seasonal tropical forests.

(e) *Changes in other factors*

Other potential directional changes could affect these ecosystems. A recent modelling study (Asner *et al.* 2001) highlighted the possibility of significant losses of critical nutrients from tropical forests that are exposed to anthropogenically enhanced nitrogen deposition, owing to complex interactions of below-ground processes. The likely increases in carbon : nitrogen ratios in plant tissue with increasing atmospheric CO₂ levels (see above), as well as parallel increases in leaf phenolics (Coley *et al.* 2002) could also negatively affect nutrient cycling in these forests. Any changes in light quality and quantity would also be likely to alter forest carbon balance (Fan *et al.* 1990; Graham *et al.* 2003). For none of these possibilities are there long-term (decade-long) ground data that could be used to evaluate the extent of ongoing change and its impact on tropical forests.

4. INTEGRATED FOREST-LEVEL RESPONSES: THE EVIDENCE SO FAR

What have been the net responses of the world's tropical rainforests to changing atmospheric composition and climate? Accurate assessment of the carbon balance of old-growth tropical rainforests in recent years is required for understanding the current global carbon cycle and for developing realistic models to project the role of this biome in the global cycle during coming decades.

Until recently, the prevailing view (e.g. Malhi & Grace 2000; Prentice *et al.* 2001; Schimel *et al.* 2001), based on multiple independent lines of evidence, has been that old-growth tropical forests are likely to have been acting as a substantial carbon sink over recent decades. Now, significant method issues and uncertainties have emerged for those data and analyses. Other evidence points to large

negative net responses of tropical rainforests to the ongoing climatic and atmospheric changes. Only some of these findings directly relate to the net carbon balance of these forests. A review of these several types of observation and their limitations reveals the uncertainty about current tropical forest carbon balance and the large gaps in our understanding.

(a) *Tropical forest responses as indicated by tree measurements*

(i) *Temporal variation in above-ground biomass*

One approach for monitoring the performance of old-growth tropical rainforests has been to infer biomass trends from long-term forest inventory plots. In such a plot, the diameters of all trees above an arbitrary minimum size are repeatedly measured. The above-ground biomass of all the trees, and thus of the plot, can then be estimated from generalized (all-species) biomass allometric equations based on harvested tropical forest trees (Brown 1997). Temporal trends are inferred by comparing biomass estimates from successive censuses.

In a study by Phillips *et al.* (1998) the authors analysed data from numerous tropical forest plots and concluded that above-ground biomass of old-growth forests had been significantly increasing in the neotropics, but not in the palaeotropics. Although such meta-analysis is potentially a valuable approach for assessing regional biomass trends, the conclusion about the neotropics was affected by inappropriate methods. As documented in a reanalysis of the dataset (Clark 2002; but see Phillips *et al.* 2002), the large inferred biomass increase in the neotropics was restricted to a substantial subset of plots with problematic data; for these plots, estimated biomass change ranged up to 7 Mg ha⁻¹ yr⁻¹ and averaged more than 2 Mg ha⁻¹ yr⁻¹. By contrast, the large sample of neotropical plots in the study that were measured with standard techniques ($n=25$) indicated no biomass increase through time (mean net change 0.3 Mg ha⁻¹ yr⁻¹, with a 95% confidence interval including 0), thus coinciding with the original finding for the palaeotropics.

A recent re-analysis of biomass trends in such plots over the past two decades (Baker *et al.* 2004) excluded many problematic plots, included a number of newer plots and probed the potential effects of several methodological issues. The authors tested different biomass allometries, including one adjusting for species differences in wood density, and they also directly addressed thorny issues arising from inappropriate and/or inadequately documented tree measurements in some plots during early years. This new analysis indicated net increases in above-ground biomass in western Amazonian forest plots on terra firme ($+0.59 \pm 0.31$ Mg C ha⁻¹ yr⁻¹) and substantially greater net increases in the potentially still-successional forest plots on river floodplains ($+1.16 \pm 0.39$ Mg C ha⁻¹ yr⁻¹), whereas only marginally significant net biomass increase ($+0.37 \pm 0.34$ Mg C ha⁻¹ yr⁻¹) was indicated for the terra firme plots in the eastern and central Amazon. For the western Amazonian plots, the data were then re-analysed to omit the trees for which growth rates had been estimated because problematic past measurements affected their increment data; with such trees removed (thus treated as if they had 0 growth), the estimated mean biomass increase for the terra firme



Figure 2. Multiple ladders are required for accurate diameter measurements of many trees in tropical forest inventory plots, both to obtain the diameter of the cylindrical bole at a permanent point of measurement above buttresses and other stem irregularities, and to avoid including vines, termite trails and other objects frequently occurring on tree boles.

and floodplain plots decreased substantially, to $0.39 \pm 0.31 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and $+0.85 \pm 0.41 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, respectively. As the authors note, assigning 0 growth to all these problematic trees may bias the results downwards. Such uncertainties will not occur with current and future measurements of these plots. Since 1998 all trees have been measured with standard best-practice techniques (Baker *et al.* 2004): using ladders to measure boles above buttresses and other irregularities (e.g. figure 2), and measuring boles at permanently marked points, with diameter tapes instead of optical instruments. The continued monitoring of these plots will provide valuable timelines on Amazonian forest dynamics and structure under changing climatic and atmospheric conditions.

A question that has been raised for the biomass trends inferred from such plots, however, is whether they are applicable to larger tropical forest landscapes. The Amazon forest plots analysed by Baker *et al.* (2004) were quite small (51 out of the 59 plots were 0.4–1.0 ha). It has been argued (Fearnside 2000; Körner 2004) that, even within a steady-state old-growth forest landscape, most local sites are accreting biomass (recovering from past disturbance), and only a very small portion of the landscape at any time is showing the large carbon losses caused by disturbance; thus a small plot sited randomly within the landscape would be most likely to be showing biomass increase. Whether the small plots that have been used to assess tropical forest biomass trends are suffering from such a bias will depend on the spatio-temporal scale(s) of the prevailing disturbance regime. Extremely rare events, such

as the mega-blowdowns that occur in central Amazonia (Nelson *et al.* 1994), may have little overall effect on biomass trends inferred from many small plots (Baker *et al.* 2004). The big issue, then, would be whether less extreme features of the disturbance regime of old-growth tropical forests are inadequately sampled by small plots.

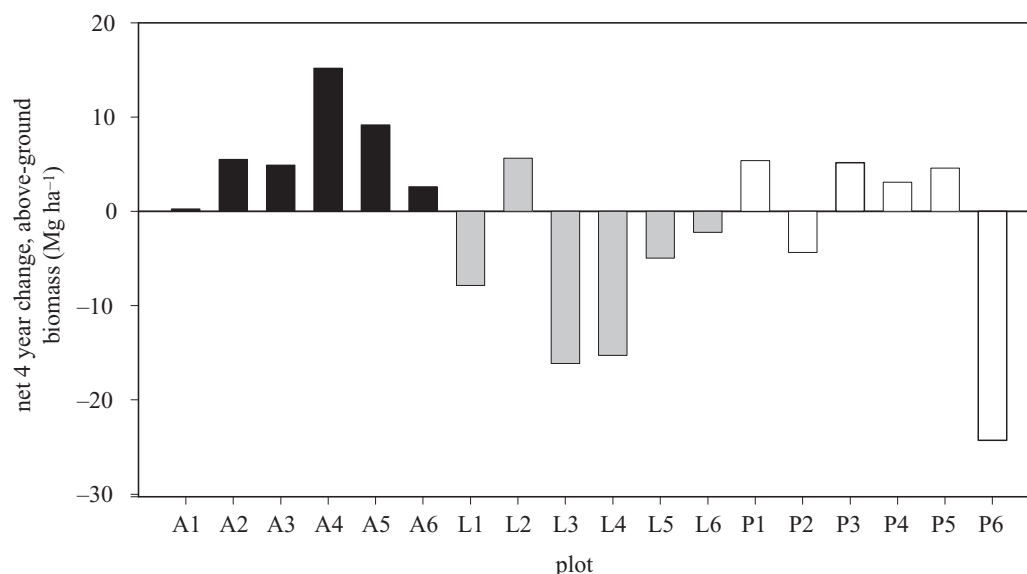
Evidence that there may be such a problem comes from three studies based on monitoring forest dynamics in numerous hectares spread out over a given tropical forest landscape. In the PDBFF (Projeto Dinâmica Biológica de Fragmentos Florestais) project in the central Amazon (Laurance *et al.* 1997), all trees that were 10 cm or more in diameter in many forest-interior 1 ha plots, were re-measured over the 12–18 years up to 1997–1999; for the 26 ha from this project that were included in the analysis of Baker *et al.* (2004, table 1), the mean estimated net biomass change over the total period was not significantly different from 0 ($+0.13 \pm 0.94 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). On Barro Colorado Island, Panama, all trees that were 1 cm or more in diameter in a 50 ha plot were re-measured over the 15 year period 1985–2000; a recent analysis of these data (Chave *et al.* 2003) similarly indicated no significant long-term change in estimated above-ground biomass in this very large plot. At La Selva, Costa Rica, all trees of 10 cm or more in diameter have been measured annually in eighteen 0.5 ha plots that were sited to sample the prevailing edaphic gradients in the old-growth landscape, based on soil/slope maps and pre-determined grid coordinates (D. B. Clark, D. A. Clark and S. F. Oberbauer, unpublished data). The net change in estimated above-ground biomass over the first 4 years of measurements (figure 3) strongly varied among the 18 plots, with most plots showing a gain in biomass, but with a few showing large net biomass losses. Across the entire 18 plot sample, estimated above-ground biomass showed no net change over the 4 year period. Given the lack of long-term biomass change found in landscape-scale studies in these three tropical forests, it appears that we need to better understand the spatio-temporal characteristics of tropical forest disturbance regimes and how they may be affecting biomass trends.

Two additional issues complicate our attempts to assess trends in above-ground biomass in these forests. One is the very large differences in wood density and architecture among tropical tree species and among tropical forest types. If there are significant floristic differences among plots or floristic changes over time within a plot, there could be large spatial or temporal differences in biomass owing to changes in the distributions of wood densities or architecture. Capturing such differences will be difficult (Chave *et al.* 2004), given that tropical forest above-ground biomass is estimated based on community-wide generalized allometric equations. The inclusion of relative wood density in such equations (Baker *et al.* 2004; Chave *et al.* 2003) is, however, a major step forward. A second issue, dealt with in few studies (Chambers *et al.* 2000; Chave *et al.* 2003), accounts for ongoing biomass losses through crown damage and branchfall; depending on the nature of the biomass allometric equation used, failing to correct for such damage can lead to significant overestimates of above-ground biomass increase (Clark *et al.* 2001).

Table 1. Elevated forest-wide tree mortality rates occurring in neotropical and palaeotropical rainforests in the strong El Niño events of 1982/1983 and 1997/1998.

(Data are for trees that are 10 cm or more in diameter; census intervals indicated in parentheses.)

	forest-wide mortality rates (percentage of stems per year)		
	non-Niño	Niño	reference
1982/1983 El Niño:			
Barro Colorado Island, Panama	1.9 (1985–1990)	3.2 (1982–1985)	Condit <i>et al.</i> (1995)
La Selva, Costa Rica	2.0 (1969–1982)	2.3 (1982–1985)	Lieberman <i>et al.</i> (1990)
1997/1998 El Niño:			
Sarawak, Malaysia	0.9 (1993–1997)	6.4 (1997/1998)	Nakagawa <i>et al.</i> (2000)
Sarawak, Malaysia	1.6 (1993–1997)	5.4 (1997/1998)	Potts (2003)
Sabah, Malaysia	0.6–1.3 (1995–1997)	1.1–5.3 (1997–1999)	Aiba & Kitayama (2002)
Manaus, Brazil	1.2 (1998/1999)	1.9 (1997/1998)	Williamson <i>et al.</i> (2001)

Figure 3. Net 4 year change (1997–2001) in estimated above-ground biomass (Mg ha^{-1}) in eighteen 0.5 ha plots stratified across an old-growth tropical wet forest landscape (the CARBONO Project plots, La Selva, Costa Rica; D. B. Clark and D. A. Clark, unpublished data). Black bars, inceptisol plots: mean change $+6.3 \text{ Mg ha}^{-1}$; grey bars, ultisol plateau plots: mean change -6.8 Mg ha^{-1} ; white bars, ultisol slope plots: mean change -1.7 Mg ha^{-1} . The above-ground biomass of each tree was estimated by using the tropical wet forest allometric equation of Brown (1997). The mean 4 year net change in estimated above-ground biomass ($n = 18$ plots) was -0.7 Mg ha^{-1} (95% confidence interval: $+3.8$ to -4.6 Mg ha^{-1}).

What do inferred trends in above-ground biomass tell us about the carbon source/sink status of tropical forests? In addition to the multiple unresolved issues discussed above, a fundamental point is that above-ground biomass is only one component of total forest carbon stocks. The other components that could be undergoing net change are above-ground fine litter, coarse woody debris, coarse roots, fine roots and soil organic carbon to depth. As shown by one recent study (Rice *et al.* 2004), adding the estimated change in just one of these other components (coarse woody debris) to the estimated change in above-ground biomass reversed the direction of estimated forest carbon balance from sink to source. Unfortunately, for no tropical forest have the necessary measurements been

made to assess the net change in total carbon stocks through time. Thus, there are no tropical forest sites for which existing plot data are sufficient to determine whether the forest is acting as a carbon sink or source.

(ii) *Interannual variation in canopy tree growth and temperature*

As noted earlier, past decades have included marked interannual climatic variation, and the responses of monitored forests to this variation could indicate how these ecosystems are responding to changes in climatic factors. Unfortunately, with one exception all the published studies based on long-term forest measurements in the tropics have been based on multi-year census intervals. When tree

responses are averaged over 2–10 year time periods, it is not possible to relate them to annual climatic variation.

In a continuing long-term study in one old-growth tropical forest (La Selva, Costa Rica), however, tree growth has been evaluated annually based on highly quality-controlled diameter measurements (Clark & Clark 1999, 2000). Analysis of this record for the 16 year period 1984–2000 (Clark *et al.* 2003) shows large coherent differences in tree growth among years. For six ecologically diverse canopy and emergent species, diameter increments of adult trees in the year of greatest growth in this period were 61–278% greater than in the year of least growth. These inter-year changes were strongly negatively related to the annual means for daily minimum temperature, even though their 16 year range was only 1.75 °C (and the growth variations were not significantly related to annual variations in either irradiance or rainfall). The greatest tree growth occurred in the two coolest years, very depressed growth rates were seen in the record-hot mega-Niño year 1997/1998, and growth rates were intermediate in the years of intermediate temperatures. Tree bole growth is considered a sensitive indicator of total tree carbon balance because of its low priority for carbon allocation (Waring & Pitman 1985; Ryan *et al.* 1996). Thus, the decrease in annual tree growth at La Selva with increased temperature points to a similar response in forest-wide primary productivity.

Independent support for this interpretation comes from plot-based estimates of forest-level above-ground biomass increment at this site. In eighteen 0.5 ha plots stratified across the La Selva old-growth landscape (the CARBONO plots; see figure 3), all trees that are 10 cm diameter or more have been annually measured since 1997. The data from the first 4 years indicated very strong interannual variation in above-ground biomass increment in these plots: the increment in the record-hot El Niño year 1997/98 was 29%, 34% and 24% lower than those of the three cooler years that followed, respectively (D. B. Clark and D. A. Clark, unpublished data).

Given that temperatures have been increasing across all tropical regions (Malhi & Wright 2004) and are projected to strongly increase in the future (see earlier discussion), this finding from La Selva is potentially applicable to tropical forests as a whole. It is possibly a conservative example, however, because La Selva is a tropical wet forest, not subject to significant drydowns. The co-occurrence of severe drought conditions with elevated temperatures in many drier parts of the tropics should be expected to amplify such temperature effects in those forests.

(iii) *Tree mortality peaks in strong El Niño events*

Tropical forest plot data from both the neotropics and the palaeotropics show large increases in forest-wide tree mortality associated with the very strong El Niño events of 1982/1983 and 1997/1998 (table 1). These events brought both elevated temperatures and extreme drought conditions to most of these study sites; for the tropical wet forest at La Selva, these were years of peak temperatures but normal or elevated rainfall.

In addition to the marked mortality spikes at the forest level (table 1), some size classes and families of trees showed particularly strong mortality responses. In

1982/1983 on Barro Colorado Island, Panama (Condit *et al.* 1995), the canopy tree species as a group showed stronger mortality increases than did shrubs, treelets or sub-canopy trees. In the central Amazon (Williamson *et al.* 2001), one species of canopy palm showed extremely high mortality in 1997/1998. The elevated mortality rates seen in trees of unburned rainforest in East Kalimantan in the 1982/1983 El Niño (Leighton & Wirawan 1986) increased with tree size: in September 1983 in ridge-top and slope plots, respectively, 37% and 71% of the trees that were more than 60 cm in diameter were found dead. A similar size-dependent mortality increase occurred in a less seasonal forest in Sarawak in 1997/1998 (Nakagawa *et al.* 2000): for the largest trees (40 cm or more in diameter), mortality rates that year were seven times those in the pre-Niño census interval. In this Sarawak forest, mortality responses varied strongly among plant families; the dominant tree family, Dipterocarpaceae, showed 31-fold higher mortality (5.3% yr⁻¹) in the El Niño year than in the prior 4 year period. In a nearby forest, Potts (2003) similarly documented large increases in tree mortality between these same time periods for the Dipterocarpaceae (2.03% yr⁻¹ versus 7.2% yr⁻¹) and Rubiaceae (2.39% yr⁻¹ versus 15.09% yr⁻¹).

Taken together, these data indicate several important levels of climatic impacts on tropical rainforests. The general finding of a sharp increase in tree mortality in the strong El Niño events of recent decades means that, around the world tropics, these old-growth forests are already being strongly negatively affected by current-time levels of temperature and drought stress. In the short-term, the elevated tree death rates during these events will translate to large transfers of carbon stocks from live biomass to coarse woody debris, with subsequent large expected increases in forest carbon emissions from decomposition (cf. Rice *et al.* 2004). The ongoing increases in both temperature and drought stress can be expected to produce increasingly severe impacts on these forests. At some point, probably far sooner than is generally recognized, the temperature regimes of even the ‘normal’ non-Niño years will have reached critically stressful levels for many tropical forests. It is also reasonable to assume that future strong Niño events, with their certainly higher temperatures and probably greater drought severity than seen in 1982/1983 and 1997/1998, will kill many more trees in these forests. Lastly, today’s old-growth tropical rainforests are carrying the imprint of the recent strong El Niño events. As shown by the above-cited studies from around the world tropics, forests have already experienced notable shifts in floristic composition and in tree size structure owing to the selective excess mortality induced by single strong El Niños. The accumulated effects of such successive events during just the next 10–20 years could profoundly change the total carbon stocks and the net carbon exchange of old-growth tropical forests.

(b) *Tropical forest responses as inferred from eddy covariance studies*

Data from a few eddy covariance (tower-based) studies of whole-forest CO₂ exchange have been interpreted as evidence that old-growth tropical rainforests are currently acting as moderate to very strong net carbon sinks (e.g.

Malhi & Grace 2000; Andreae *et al.* 2002). The published tropical forest eddy covariance analyses so far have been based on 17 days to 10 months of data from four Amazonian rainforest sites (Fan *et al.* 1990; Grace *et al.* 1995; Malhi *et al.* 1998; Andreae *et al.* 2002; Araújo *et al.* 2002; Carswell *et al.* 2002) and on 3 years of measurements at a tropical wet forest site in Costa Rica (Loescher *et al.* 2003). Using widely accepted practices to estimate net forest CO₂ exchange from the data, all these studies produced estimates of significant net CO₂ uptake by these tropical rainforests, all of which were assumed to be old growth.

Multiple recent lines of evidence, however, have raised significant questions about such eddy covariance estimates of tropical forest CO₂ exchange. A major problem for the use of this technique in this biome is the overwhelming predominance of still air conditions at night (*ca.* 80% of nights (Loescher *et al.* 2003) and 92% of night hours (Goulden *et al.* 2001)), and the resulting need to filter out data from the many periods when these conditions make the eddy covariance technique inoperable. As shown by Araújo *et al.* (2002) and Miller *et al.* (2004) for eastern and central Amazonian forests, the same eddy covariance dataset for a given forest indicates NEE values that differ by more than 4 Mg C ha⁻¹ yr⁻¹, depending on the treatment of the data from periods of still air. Recent studies combining biometric and eddy covariance approaches now point to the forests being a net CO₂ source or, at most, a quite small sink (Anonymous 2003; Miller *et al.* 2004). In addition, the tropical forest eddy covariance studies have been focused uniquely on CO₂ and therefore have missed forest carbon losses in the form of BVOCs: tropical forests can emit large amounts of these compounds (Fan *et al.* 1990; Geron *et al.* 2002). Given these issues, confidence cannot be placed in either the magnitude or the sign of the eddy covariance estimates so far of tropical forest carbon balance.

Eddy covariance measurements can, however, be valuable for indicating some features of how these forests perform under different climatic conditions. For example, from their eddy covariance data for a Brazilian Amazonian forest, Lloyd, Grace and colleagues (Grace *et al.* 1995, 1996b; Lloyd *et al.* 1995) developed a model of forest carbon exchange as a function of climatic factors; the model indicated abrupt declines in GPP at temperatures more than 1.3 °C above those in the year of their measurements. As they noted, their measurement year, 1992/1993, was anomalously cool; further, their 55 days of measurements included four extreme cold events ('friagens'). Their model also indicated that forest carbon losses from respiration would exceed carbon uptake at temperatures only 1.2 °C above those in 1992/1993. As the authors pointed out, although these model results are based on numerous assumptions and on limited direct data, they suggest a high degree of sensitivity of the carbon balance of that forest to even small temperature increases. Such temperature sensitivity was also indicated by the daytime net CO₂ fluxes estimated by eddy covariance at La Selva, Costa Rica (Loescher *et al.* 2003). After data for net daytime CO₂ exchange were related to light, the residuals from that relationship were plotted against air temperature: at temperatures above 20–26 °C, there was an increased frequency of positive residuals, indicating reduced daytime

carbon uptake at the higher temperatures. The La Selva eddy covariance data also indicated large interannual differences in forest net carbon balance (Loescher *et al.* 2003): when these estimates were extended to the local climatic variation in the 1997/1998 El Niño year, they projected greatly depressed net carbon uptake in that record-hot year, compared with the uptake estimated for the two cooler years that followed (H. Loescher and S. F. Oberbauer, unpublished data).

(c) *Tropical forest performance inferred from atmospheric inversion calculations*

Another type of evidence that could help establish the current responses of tropical rainforests are inversion calculations based on the CO₂ (or O₂:N₂) concentrations and isotopic variation in atmospheric gas samples being collected at sites around the world. An inversion calculation involves a model based on current best understanding of the processes involved in the uptake and emissions of carbon (or oxygen) by the world's oceans and terrestrial ecosystems, combined with a model of global atmospheric transport. The results are adjusted (essentially back-fitted, hence the term 'inverse calculation') to most closely fit the spatial and temporal patterns in the actual gas sample data. The calculation provides quantitative estimates of the net carbon (or oxygen) fluxes between the atmosphere on the one hand, and the oceans and land ecosystems on the other hand, for the period covered by the atmospheric gas samples.

Before considering the results of inversion calculations, it is instructive to review what is known unambiguously about the temporal changes in global atmospheric CO₂ concentrations. As highlighted some time ago by Woodwell (1986, 1995), the large annual oscillation in the record of long-term rise in atmospheric CO₂ at Mauna Loa (Keeling *et al.* 1995) reflects the metabolism of northern forests: their carbon uptake dominates ecosystem carbon exchange in the northern growing season, respiration dominates in the winter, and these seasonal changes produce a clear signal in the atmosphere. The amplitude of this oscillation in atmospheric CO₂ concentration declines from the Arctic to the South Pole (Keeling *et al.* 2001), reflecting the different phenologies and proportional contributions of vegetation in different parts of the world. Woodwell (1986, 1995) emphasized that this seasonal oscillation is unequivocal evidence of rapid large effects on atmospheric CO₂ levels from changes in the relationship between photosynthesis and respiration in terrestrial ecosystems; this means that shifts in the photosynthesis:respiration ratio of global vegetation could greatly affect the rate and level of CO₂ accumulation in the atmosphere. He then pointed out that plant respiration and heterotrophic respiration can respond to temperature more strongly than does photosynthesis; as temperatures rise, such decreases in the photosynthesis:respiration ratio of global terrestrial ecosystems will increase atmospheric CO₂ concentrations and will thus constitute a biotic positive feedback to the warming. A recent analysis of atmospheric carbon dynamics by Houghton *et al.* (1998) reinforced this scenario.

In addition to the seasonal oscillation in atmospheric [CO₂], there has been strong interannual variation (Keeling *et al.* 2001; Prentice *et al.* 2001) in the

atmospheric CO₂ anomaly, which is the temporal variation in the rate of increase in atmospheric [CO₂], beyond the effects of annual fossil fuel emissions. Whereas in some years less than half of the current fossil fuel emissions to the atmosphere were retained as a net gain in atmospheric [CO₂], in other years the net gain nearly equalled the year's global fossil fuel emissions. Over the past two decades, the peaks in the atmospheric CO₂ anomaly have all occurred at times of peak global temperatures, which have largely coincided with El Niño events (Keeling *et al.* 2001). The 1997/1998 El Niño brought the highest rate of increase in atmospheric CO₂ ever measured, 6.0 Pg (= 6 × 10¹⁵ g) C yr⁻¹ (Keeling *et al.* 2001; Prentice *et al.* 2001). These two atmospheric findings—the seasonal oscillation, and the interannual variation in the atmospheric CO₂ anomaly and its relationship to temperature and to El Niño—are well constrained by the data.

Much less certain, however, are the inferences from atmospheric inversion model calculations about the relative contributions of the oceans and the land, and of different latitudinal belts, to this interannual variation in the atmospheric CO₂ anomaly. As noted earlier, these calculations are based on: vegetation and oceanic process models, which include many assumptions and hypotheses; models of atmospheric transport, which are equally uncertain; uncertain estimates of the land areas of different vegetation types and of the relative roles of C₃ and C₄ plants; and gas sample measurements, with their own uncertainties and varying degrees of cross-calibration. In addition, the atmospheric inversion models so far have been based on different kinds of data (CO₂, O₂:N₂, ¹³C/¹²C), collected at different sets of sampling sites and over differing periods, and have involved significantly different approaches (see Gurney *et al.* 2002).

Findings from many such inversion models have been recently reviewed (Houghton 2001; Prentice *et al.* 2001). Most studies so far have indicated that the decadal averaged net carbon flux from the terrestrial tropics during 1980–1996 has been on the order of -1 (sink) to +1.5 (source) Pg C yr⁻¹. Given that tropical deforestation has been estimated as a net decadal averaged flux on the order of +1.5 to +1.7 Pg C yr⁻¹ during these years (Houghton 2001), most of these estimates of net tropical carbon flux point to a counteracting net carbon sink in tropical vegetation.

A very different view, however, emerges from the annual estimates produced by a recent inversion calculation (Keeling & Piper 2001; Clark *et al.* 2003). This analysis is the first to be based on both atmospheric CO₂ concentrations and ¹³C/¹²C isotopic composition in weekly atmospheric samples collected from the Arctic to the South Pole over a long time period (1978–2000). According to this analysis, the terrestrial tropics dominated the strong variation in the atmospheric CO₂ anomaly over the past two decades; the estimated net carbon flux from the terrestrial tropics varied over this period from a net sink of -1.8 Pg C yr⁻¹ to a net source of +6.7 Pg C yr⁻¹, and this strong interannual variation was linked to the interannual changes in mean tropical temperature and rainfall. The inferred contribution of the terrestrial tropics to the atmospheric CO₂ anomaly was greatest in the years of peak temperatures (and anomalously low rainfall in many tropical areas); most of these were El Niño years.

Given the uncertainties in inversion model calculations and in the data that underlie them, there is a clear need to test these differing estimates against direct observations of other types. Independently obtained data that are consistent with inversion results will lead to increased confidence in a given set of inferences about the carbon fluxes from different parts of the world.

There is now one case of such independent corroboration. In a joint analysis (Clark *et al.* 2003), we have found that the interannual variation in tree growth at La Selva during the period 1984–2000 (see above) is highly significantly negatively correlated with the tropical terrestrial component of the atmospheric CO₂ anomaly as inferred for this period in the Keeling *et al.* (2001) inverse calculation analysis. Years of anomalously poor tree growth at La Selva were years of peak inferred net emissions from the terrestrial tropics, and both of these records were significantly related to annual temperatures and El Niño. Such a relationship has been independently projected by three vegetation process models (Kindermann *et al.* 1996; Gerard *et al.* 1999; Ito & Oikawa 2000): in these simulations, temperature-driven variations in the NPP of tropical evergreen forests dominated the terrestrial component of the atmospheric CO₂ anomaly. Further empirical support for such a relationship between tropical NPP and temperature comes from three recent remote-sensing studies (Braswell *et al.* 1997; Asner *et al.* 2000; Los *et al.* 2001): in all three analyses, satellite-derived measures of vegetation greenness (NDVI, normalized difference vegetation index) indicated reduced productivity in tropical ecosystems in warmer years.

Although this first case of agreement among independent approaches is encouraging, much is still needed before there will be a robust understanding of the processes underlying the atmospheric CO₂ anomaly (see Schimel *et al.* 2001). The sparse atmospheric sampling in tropical regions needs to be expanded (Gurney *et al.* 2002). The interannual and spatial variations in carbon emissions from tropical land-use change need to be more precisely quantified (cf. Houghton 2001). Long-term (10 years or more) records of annual forest performance from other tropical forest sites are currently lacking and are critically needed. Extensive empirical data are also needed for evaluating the temporal patterns in ¹³C/¹²C discrimination by terrestrial plants (Keeling & Piper 2001).

5. CURRENT AND FUTURE SINKS OR SOURCES? CONCLUSIONS BASED ON THE EVIDENCE IN HAND

The studies reviewed here present a new perspective on the role of tropical rainforests in the global carbon budget. The earlier view of this biome as a CO₂-stimulated carbon sink seemed to be well founded on diverse lines of evidence: plot-based biomass estimates, eddy covariance studies and inferences from atmospheric inversion calculations. As seen in this review, however, these findings are now found to involve large uncertainties and questions related to methods and interpretation. Change in above-ground biomass is just one component of net forest carbon balance, and in no tropical rainforest has a complete assessment been made of total carbon stocks and their

change through time. Although the eddy covariance technique can tell us much about forest metabolism and its response to climate variation, it is now generally recognized that the existing eddy covariance estimates of tropical forest uptake may be subject to significant methods artefacts. Finally, although multiple atmospheric inversion models have indicated that tropical old-growth forests may have been a significant net carbon sink in recent decades, others have not, and this approach involves many uncertainties. The bottom line currently is that existing data are insufficient to establish whether the world's tropical rainforests are currently net carbon sinks, net carbon sources or are in carbon balance.

Accumulating evidence, however, points to potentially large negative impacts on this biome in the future from the ongoing climatic and atmospheric changes. Although the more realistic experiments with elevated CO₂ have shown no biomass increases in tropical forest trees, they revealed a build-up in leaf and twig TNC concentrations; such a decrease in plant tissue quality is likely to affect nutrient cycling and reduce forest productivity. Studies from the leaf- to the stand-level indicate that, as temperatures continue to rise, tropical forests are likely to respond with substantial reductions in NPP and elevated tree mortality. Continued increases in drought severity in the more seasonal tropical forests would compound these temperature effects. Taken together, many findings suggest that tropical old-growth forests will be acting as strongly increasing net sources of atmospheric CO₂ as warming proceeds.

6. A RESEARCH AGENDA

Understanding the Earth system, in all of its fascinating complexity, is the most important scientific adventure of our time. We should get on with it, as free as possible from our preconceptions of the way the world ought to work.

(Kirchner 2002, p. 406)

Given the key roles of the tropical forest biome in the global carbon cycle and in terms of biodiversity and environmental services, intensified research is urgently needed to establish what is currently happening to these forests and to provide the process-level understanding needed to project their likely future. Several high priorities can be identified for such research: (i) long-term (multi-decade) monitoring of forest structure and function around the world tropics, with special attention given to poorly documented tropical forest areas (e.g. Africa); (ii) monitoring of processes at annual or shorter time intervals in representative forests, so that ecosystem responses can be related to interannual climatic and atmospheric variation; (iii) repeated assessment of all carbon stocks in representative forests, to ground-check their sink/source status; (iv) whole-forest experiments to test the effects of increased temperature and CO₂ concentration, ideally with three treatment levels (to capture the likely nonlinear responses (Körner 1995*b*)); and (v) clearly documenting the data from this research and making it publicly accessible, as has been done for other globally significant data (e.g. the human genome project). Such a multi-pronged research effort could go a long way towards revealing the present and future responses of the world's tropical rainforests to the immense global changes currently underway.

While writing this essay I was partly supported by grants from the National Science Foundation (LTREB DEB-0129038, DEB 0108389, Geosciences 0223284) and the Andrew W. Mellon Foundation; the CARBONO results reported here were also partly supported by grants from the National Science Foundation (DEB 9629245) and the Department of Energy (DE-FG02-96ER62289). I thank NSF for its long-term support of the La Selva Biological Station and David B. Clark for his input during the development of this paper.

REFERENCES

- Aiba, S.-I. & Kitayama, K. 2002 Effects of the 1997–98 El Niño drought on rain forests of Mount Kinabalu, Borneo. *J. Trop. Ecol.* **18**, 215–230.
- Albritton, D. L. (and 58 others) 2001 Technical summary. In *Climate change 2001: the scientific basis* (ed. J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell & C. A. Johnson), pp. 21–83. Cambridge University Press.
- Amthor, J. S. & Baldocchi, D. D. 2001 Terrestrial higher plant respiration and net primary production. In *Terrestrial global productivity* (ed. J. Roy, B. Saugier & H. A. Mooney), pp. 33–59. San Diego, CA: Academic.
- Andreae, M. O. (and 22 others) 2002 Biogeochemical cycling of carbon, water, energy, trace gases, and aerosols in Amazonia: the LBA-EUSTACH experiments. *J. Geophys. Res.* **107**, 8066–8090. (DOI 10.1029/2001JD000524.)
- Anonymous 2003 Fluxo invertido: após sucessivos ocorrências do El Niño nos anos 90, a Floresta Nacional do Tapajós libera mais gás carbônico do que absorve. *Pesquisa FAPESP* **88**, 50–51.
- Araújo, A. C. (and 11 others) 2002 Comparative measurements of carbon dioxide fluxes from two nearby towers in a central Amazonian rainforest: the Manaus LBA site. *J. Geophys. Res.* **107**, 8090–8109. (DOI 10.1029/2001JD000676.)
- Arnone, J. A. I. 1996 Predicting responses of tropical plant communities to elevated CO₂: lessons from experiments with model ecosystems. In *Carbon dioxide, populations, and communities* (ed. C. Körner & F. A. Bazzaz), pp. 101–121. London: Academic.
- Asner, G. P., Townsend, A. R. & Braswell, B. H. 2000 Satellite observation of El Niño effects on Amazon forest phenology and productivity. *Geophys. Res. Lett.* **27**, 981–984.
- Asner, G. P., Townsend, A. R., Riley, W. J., Matson, P. A., Neff, J. C. & Cleveland, C. C. 2001 Physical and biogeochemical controls over terrestrial ecosystem responses to nitrogen deposition. *Biogeochemistry* **54**, 1–39.
- Baker, T. R. (and 17 others) 2004 Increasing biomass in Amazonian forest plots. *Phil. Trans. R. Soc. Lond. B* (In this issue.) (DOI 10.1098/rstb.2003.1422.)
- Baldocchi, D. D. & Amthor, J. S. 2001 Canopy photosynthesis: history, measurements, and models. In *Terrestrial global productivity* (ed. J. Roy, B. Saugier & H. A. Mooney), pp. 9–31. San Diego, CA: Academic.
- Bazzaz, F. A. 1998 Tropical forests in a future climate: changes in biological diversity and impact on the global carbon cycle. *Climate Change* **39**, 317–336.
- Bounoua, L. (and 10 others) 1999 Interactions between vegetation and climate: radiative and physiological effects of doubled atmospheric CO₂. *J. Climate* **12**, 309–324.
- Braswell, B. H., Schimel, D. S., Linder, E. & Moore III, B. 1997 The response of global terrestrial ecosystems to interannual temperature variability. *Science* **278**, 870–872.
- Brown, S. 1997 Estimating biomass and biomass change of tropical forests: a primer. Forestry paper 134. Rome: United Nations Food and Agriculture Organization.
- Carswell, F. E. (and 10 others) 2002 Seasonality in CO₂ and H₂O flux at an eastern Amazonian rain forest. *J. Geophys. Res.* **107**, 8076–8090. (DOI 10.1029/2000JD000284.)

- Ceulemans, R., Janssens, I. A. & Jach, M. E. 1999 Effects of CO₂ enrichment on trees and forests: lessons to be learned in view of future ecosystem studies. *Ann. Bot.* **84**, 577–590.
- Chambers, J. Q., DosSantos, J., Ribeiro, R. J. & Higuchi, N. 2000 Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *Forest Ecol. Mgmt* **5348**, 1–12.
- Chave, J., Condit, R., Lao, S., Caspersen, J. P., Foster, R. B. & Hubbell, S. P. 2003 Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *J. Ecol.* **91**, 240–252.
- Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S. & Perez, R. 2004 Error propagation and scaling for tropical forest biomass estimates. *Phil. Trans. R. Soc. Lond. B* (In this issue.) (DOI 10.1098/rstb.2003.1425.)
- Chen, J., Carlson, B. E. & Del Genio, A. D. 2002 Evidence for strengthening of the tropical general circulation in the 1990s. *Science* **295**, 838–841.
- Clark, D. A. 2002 Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecol. Applic.* **12**, 3–7.
- Clark, D. A. & Clark, D. B. 1999 Assessing the growth of tropical rain forest trees: issues for forest modeling and management. *Ecol. Applic.* **9**, 981–997.
- Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R. & Ni, J. 2001 Measuring net primary production in forests: concepts and field methods. *Ecol. Applic.* **11**, 356–370.
- Clark, D. A., Piper, S. C., Keeling, C. D. & Clark, D. B. 2003 Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proc. Natl Acad. Sci. USA* **100**, 5852–5857.
- Clark, D. B. & Clark, D. A. 2000 Tree growth, mortality, physical condition, and microsite in old-growth lowland tropical rain forest. *Ecol. Arch.* <http://www.esapubs.org/archive/ecol/E081/003/default.htm>.
- Cole, J. 2001 A slow dance for El Niño. *Science* **291**, 1496–1497.
- Coley, P. D., Massa, M., Lovelock, C. E. & Winter, K. 2002 Effects of elevated CO₂ on foliar chemistry of saplings of nine species of tropical tree. *Oecologia* **133**, 62–69.
- Condit, R., Hubbell, S. P. & Foster, R. B. 1995 Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol. Monogr.* **65**, 419–439.
- Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. & Totterdell, I. J. 2000 Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184–187.
- Crutzen, P. J., Fall, R., Galbally, I. & Lindinger, W. 1999 Parameters for global ecosystem models. *Nature* **399**, 535.
- Crutzen, P. J. (and 10 others) 2000 High spatial and temporal resolution measurements of primary organics and their oxidation products over the tropical forests of Surinam. *Atmos. Environ.* **34**, 1161–1165.
- Cunningham, S. C. & Read, J. 2003 Do temperate rainforest trees have a greater ability to acclimate to changing temperatures than tropical rainforest trees? *New Phytol.* **157**, 55–64.
- Easterling, D. R. (and 10 others) 1997 Maximum and minimum temperature trends for the globe. *Science* **277**, 364–367.
- Fan, S.-M., Wofsy, S. C., Bakwin, P. S. & Jacob, D. J. 1990 Atmosphere–biosphere exchange of CO₂ and O₃ in the central Amazon forest. *J. Geophys. Res.* **95**, 16 851–16 864.
- Fearnside, P. M. 2000 Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. *Climate Change* **46**, 115–158.
- Fedorov, A. V. & Philander, S. G. 2000 Is El Niño changing? *Science* **288**, 1997–2002.
- Field, C. B. 2001 Plant physiology of the ‘missing’ carbon sink. *Pl. Physiol.* **125**, 25–28.
- Field, C. B., Behrenfeld, M. J., Randerson, J. T. & Falkowski, P. 1998 Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* **281**, 237–240.
- Fitter, A. H. & Hay, R. K. M. 1981 *Environmental physiology of plants*. London: Academic.
- Folland, C. K. (and 148 others) 2001 Observed climate variability and change. In *Climate change 2001: the scientific basis* (ed. J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell & C. A. Johnson), pp. 99–181. Cambridge University Press.
- Gerard, J. C., Nemry, B., Francois, L. M. & Warnant, P. 1999 The interannual change of atmospheric CO₂: contribution of subtropical ecosystems? *Geophys. Res. Lett.* **26**, 243–246.
- Geron, C., Guenther, A., Greenberg, J., Loeschner, H. W., Clark, D. & Baker, B. 2002 Biogenic volatile organic compound emissions from a lowland tropical wet forest in Costa Rica. *Atmos. Environ.* **36**, 3793–3802.
- Gifford, R. M. 2003 Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. *Funct. Pl. Biol.* **30**, 171–186.
- Goulden, M. L., Miller, S. D., Menton, M. C., Litvak, M. E., Rocha, H. R., Freitas, H. & Oviedo, A. 2001 *Measuring the effect of selective logging on forest–atmosphere exchange*. Atlanta, GA: LBA All-Scientists Meeting.
- Grace, J. (and 11 others) 1995 Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992 to 1993. *Science* **270**, 778–780.
- Grace, J., Lloyd, J., McIntyre, J., Miranda, A. C., Meir, P. & Miranda, H. S. 1996a Carbon dioxide flux over Amazonian rain forest in Rondonia. In *Amazonian deforestation and climate* (ed. J. H. C. Gash, C. A. Nobre, J. M. Roberts & R. L. Victoria), pp. 307–318. Chichester: Wiley.
- Grace, J., Malhi, Y., Lloyd, J., McIntyre, J., Miranda, A. C., Meir, P. & Miranda, H. S. 1996b The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. *Global Change Biol.* **2**, 209–217.
- Graham, E. A., Mulkey, S. S., Kitajima, K., Phillips, N. G. & Wright, S. J. 2003 Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. *Proc. Natl Acad. Sci. USA* **100**, 572–576.
- 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.
- Gurney, K. R. (and 25 others) 2002 Towards robust regional estimates of CO₂ sources and sinks using atmospheric transport models. *Nature* **415**, 626–630.
- Hammond, D. S. & ter Steege, H. 1998 Propensity for fire in Guianan rainforests. *Conserv. Biol.* **12**, 944–947.
- Harley, P. C., Monson, R. K. & Lerdau, M. T. 1999 Ecological and evolutionary aspects of isoprene emission from plants. *Oecologia* **118**, 109–123.
- Harrison, R. D. 2001 Drought and the consequences of El Niño in Borneo: a case study of figs. *Popul. Ecol.* **43**, 63–75.
- Hoffert, M. I. (and 17 others) 2002 Advanced technology paths to global climate stability: energy for a greenhouse planet. *Science* **298**, 981–987.
- Hogan, K. P., Smith, A. P. & Ziska, L. H. 1991 Potential effects of elevated CO₂ and changes in temperature on tropical plants. *Pl. Cell Environ.* **14**, 763–778.
- Holland, E. A., Neff, J. C., Townsend, A. R. & McKeown, B. 2000 Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: implications for models. *Global Biogeochem. Cycles* **14**, 1137–1151.
- Houghton, R. A. 2001 Global terrestrial productivity and carbon balance. In *Terrestrial global productivity* (ed. J. Roy, B. Saugier & H. A. Mooney), pp. 499–520. San Diego, CA: Academic.

- Houghton, R. A., Davidson, E. A. & Woodwell, G. M. 1998 Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance. *Global Biogeochem. Cycles* **12**, 25–34.
- Huc, R. & Guehl, J. M. 1989 Environmental control of CO₂ assimilation rate and leaf conductance in two species of the tropical rain forest of French Guiana (*Jacaranda copaia* D. Don and *Eperua falcata* Aubl.). *Ann. Sci. Forestières* **46**(Suppl. 1), 443s–447s.
- Ishida, A., Toma, T., Matsumoto, Y., Yap, S. K. & Maruyama, Y. 1996 Diurnal changes in leaf gas exchange characteristics in the uppermost canopy of a rain forest tree, *Dryobalanops aromatica* Gaertn. f. *Tree Phys.* **16**, 779–785.
- Ito, A. & Oikawa, T. 2000 A model analysis of the relationship between climate perturbations and carbon budget anomalies in global terrestrial ecosystems: 1970 to 1997. *Climate Res.* **15**, 161–183.
- Keeling, C. D. & Piper, S. C. 2001 Exchanges of atmospheric CO₂ and ¹³CO₂ with the terrestrial biosphere and oceans from 1978 to 2000. IV. Critical overview. *S. I. O. Ref. Series* **01-09**, 1–23.
- Keeling, C. D., Whorf, T. P., Wahlen, M. & Van der Plicht, J. 1995 Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* **375**, 666–670.
- Keeling, C. D., Piper, S. C., Bacastow, R. B., Wahlen, M., Whorf, T. P., Heimann, M. & Meijer, H. A. 2001 Exchanges of atmospheric CO₂ and ¹³CO₂ with the terrestrial biosphere and oceans from 1978 to 2000. I. Global aspects. *S. I. O. Ref. Series* **01-06**, 1–45.
- Keller, M. & Lerdau, M. 1999 Isoprene emission from tropical forest canopy leaves. *Global Biogeochem. Cycles* **13**, 19–29.
- Kindermann, J., Wurth, G. & Kohlmaier, G. H. 1996 Interannual variation of carbon exchange fluxes in terrestrial ecosystems. *Global Biogeochem. Cycles* **10**, 737–755.
- Kirchner, J. W. 2002 The Gaia hypothesis: fact, theory, and wishful thinking. *Climate Change* **52**, 391–408.
- Kirschbaum, M. U. F., Simioni, G., Medlyn, B. E. & McMurtrie, R. E. 2003 On the importance of including soil nutrient feedback effects for predicting ecosystem carbon exchange. *Funct. Pl. Biol.* **30**, 223–237.
- 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 Phys.* **14**, 347–360.
- Körner, C. 1995a Biodiversity and CO₂: global change is under way. *Gaia* **4**, 234–243.
- Körner, C. 1995b Towards a better experimental basis for upscaling plant responses to elevated CO₂ and climate warming. *Pl. Cell Environ.* **18**, 1101–1110.
- Körner, C. 1998 Tropical forests in a CO₂-rich world. *Climate Change* **39**, 297–315.
- Körner, C. 2001 Experimental plant ecology: some lessons from global change research. In *Ecology: achievement and challenge* (ed. M. C. Press, N. J. Huntly & S. Levin), pp. 227–247. Oxford: Blackwell Science.
- Körner, C. 2004 Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Phil. Trans. R. Soc. Lond. B* (In this issue) (DOI 10.1098/rstb.2003.1429.)
- Laurance, W. F. & Williamson, G. B. 2001 Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conserv. Biol.* **15**, 1529–1535.
- 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.
- Leigh Jr, E. G., Windsor, D. M., Rand, A. S. & Foster, R. B. 1990 The impact of the ‘El Niño’ drought of 1982–83 on a Panamanian semideciduous forest. In *Global ecological consequences of the 1982–83 El Niño–Southern Oscillation* (ed. P. W. Glynn), pp. 473–486. Amsterdam: Elsevier.
- Leighton, M. & Wirawan, N. 1986 Catastrophic drought and fire in Borneo tropical rain forest associated with the 1982–1983 El Niño Southern Oscillation event. In *Tropical rain forests and the world atmosphere* (ed. G. T. Prance), pp. 75–102. Boulder, CO: Westview Press.
- Lerdau, M., Guenther, A. & Monson, R. 1997 Plant production and emission of volatile organic compounds. *Bioscience* **47**, 373–383.
- Lerdau, M. T. & Throop, H. L. 1999 Isoprene emission and photosynthesis in a tropical forest canopy: implications for model development. *Ecol. Applic.* **9**, 1109–1117.
- Lieberman, D., Hartshorn, G. S., Lieberman, M. & Peralta, R. 1990 Forest dynamics at La Selva Biological Station, 1969–1985. In *Four neotropical rainforests* (ed. A. H. Gentry), pp. 509–521. New Haven, CT: Yale University Press.
- Lloyd, J., Grace, J., Miranda, A. C., Meir, P., Wong, S. C., Miranda, H. S., Wright, I. R., Gash, J. H. C. & McIntyre, J. 1995 A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties. *Pl. Cell Environ.* **18**, 1129–1145.
- Loescher, H. W., Oberbauer, S. F., Gholz, H. L. & Clark, D. B. 2003 Environmental controls on net ecosystem-level exchange of carbon and their potential consequences for productivity in wet tropical forests of central America. *Global Change Biol.* **9**, 396–412.
- Los, S. O., Collatz, G. J., Bounoua, L., Sellers, P. J. & Tucker, C. J. 2001 Global interannual variations in sea surface temperature and land surface vegetation, air temperature, and precipitation. *J. Climate* **14**, 1535–1549.
- Lovelock, C. E., Winter, K., Mersits, R. & Popp, M. 1998 Responses of communities of tropical tree species to elevated CO₂ in a forest clearing. *Oecologia* **116**, 207–218.
- Lovelock, C. E., Virgo, A., Popp, M. & Winter, K. 1999 Effects of elevated CO₂ concentrations on photosynthesis, growth and reproduction of branches of the tropical canopy tree species, *Luehea seemannii* Tr. & Planch. *Pl. Cell Environ.* **22**, 49–59.
- Malhi, Y. & Grace, J. 2000 Tropical forests and atmospheric carbon dioxide. *Trends Ecol. Evol.* **15**, 332–337.
- Malhi, Y. & Wright, J. 2004 Spatial patterns and recent trends in the climate of tropical forest regions. *Phil. Trans. R. Soc. Lond. B* (In this issue.) (DOI 10.1098/rstb.2003.1433.)
- Malhi, Y., Nobre, A. D., Grace, J., Kruijff, B., Pereira, M. G. P., Culf, A. & Scott, S. 1998 Carbon dioxide transfer over a central Amazonian rain forest. *J. Geophys. Res.* **103**, 31 593–31 612.
- 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 production. *Nature* **363**, 234–240.
- Miller, S. D., Goulden, M. L., Menton, M. C., da Rocha, H. R., Freitas, H. C., Michela e Silva Figueira, A. & Dias de Sousa, C. A. 2004 Biometric and micrometeorological measurements of tropical forest carbon balance. *Ecol. Applic.* **14**. (In the press.)
- Nakagawa, M. (and 12 others) 2000 Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. *J. Trop. Ecol.* **16**, 355–367.
- 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.

- Nemani, R. R., Keeling, C. D., Hashimoto, H., Jolly, W. M., Piper, S. C., Tucker, C. J., Myrneni, R. B. & Running, S. W. 2003 Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* **300**, 1560–1563.
- Nepstad, D. C. (and 19 others) 2002 The effects of partial throughfall exclusion on canopy processes, above ground production, and biogeochemistry of an Amazon forest. *J. Geophys. Res.* **107**, 1–18.
- Oberbauer, S. F. 1983 The ecophysiology of *Pentaclethra macroleoba*, a canopy tree species in the rainforests of Costa Rica. PhD thesis, Duke University, Durham, NC, USA.
- O'Neill, B. C. & Oppenheimer, M. 2002 Dangerous climate impacts and the Kyoto Protocol. *Science* **296**, 1971–1972.
- Page, S. E., Siegert, F., Rieley, J. O., Boehm, H.-D. V., Jaya, A. & Limin, S. 2002 The amount of carbon released from peat and forest fires in Indonesia during 1997. *Nature* **420**, 61–65.
- 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. (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 13 others) 2002 Changes in growth of tropical forests: evaluating potential biases. *Ecol. Applic.* **12**, 576–587.
- Potts, M. D. 2003 Drought in a Bornean everwet rain forest. *J. Ecol.* **91**, 467–474.
- Prentice, I. C., Farquhar, G. D., Fasham, M. J. R., Goulden, M. L., Heimann, M., Jaramillo, V. J., Khashgi, H. S., Le Quere, C., Scholes, R. J. & Wallace, D. W. R. 2001 The carbon cycle and atmospheric carbon dioxide. In *Climate change 2001: the scientific basis* (ed. J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell & C. A. Johnson), pp. 183–237. Cambridge University Press.
- Read, J. 1990 Some effects of acclimation temperature on net photosynthesis in some tropical and extra-tropical Australasian *Nothofagus* species. *J. Ecol.* **78**, 100–112.
- Rice, A. H., Pyle, E. H., Saleska, S. R., Hutyrá, L., Palace, M., Keller, M., de Camargo, P. B., Portilho, K., Marques, D. F. & Wofsy, S. C. 2004 Carbon balance and vegetation dynamics in an old-growth Amazonian forest. *Ecol. Applic.* **14**. (In the press.)
- Roderick, M. L. & Farquhar, G. D. 2002 The cause of decreased pan evaporation over the past 50 years. *Science* **298**, 1410–1411.
- Roderick, M. L., Farquhar, G. D., Berry, S. L. & Noble, I. R. 2001 On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia* **129**, 21–30.
- Rosenthal, Y. 1998 Variations of ecosystem gas exchange in the rain forest mesocosm at Biosphere 2 in response to elevated CO₂. *Global Change Biol.* **4**, 539–547.
- Rowland-Bamford, A. J. 2000 Plant responses to changing carbon dioxide and temperature. In *Trace gas emissions and plants* (ed. S. N. Singh), pp. 63–74. Dordrecht, The Netherlands: Kluwer.
- Ryan, M. G., Hubbard, R. M., Clark, D. A. & Sanford Jr, R. L. 1994a Woody-tissue respiration for *Simarouba amara* and *Miconia guianensis*, two tropical rain forest trees with different growth habits. *Oecologia* **100**, 213–220.
- Ryan, M. G., Linder, S., Vose, J. M. & Hubbard, R. M. 1994b Dark respiration of pines. *Ecol. Bull.* **43**, 50–63.
- Ryan, M. G., Hunt Jr, E. R., McMurtrie, R. E., Agren, G. I., Aber, J. D., Friend, A. D., Rastetter, E. B., Pulliam, W. M., Raison, R. J. & Linder, S. 1996 Comparing models of ecosystem function for temperate conifer forests. I. Model description and validation. In *Global change: effects on coniferous forests and grasslands* (ed. A. I. Breymer, D. O. Hall, J. M. Melillo & G. I. Agren), pp. 313–362. Indianapolis, IN: Wiley.
- Salafsky, N. 1998 Drought in the rain forest. Part II: an update based on the 1994 ENSO event. *Climate Change* **39**, 601–603.
- Saxe, H., Cannell, M. G. R., Johnsen, O., Ryan, M. G. & Vourlitis, G. 2001 Tree and forest functioning in response to global warming. *New Phytol.* **149**, 369–400.
- Schimel, D. S. (and 29 others) 2001 Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* **414**, 169–172.
- Sharkey, T. D. & Yeh, S. 2001 Isoprene emission from plants. *A. Rev. Pl. Physiol. Pl. Mol. Biol.* **52**, 407–436.
- Siegert, F., Ruecker, G., Hinrichs, A. & Hoffmann, A. A. 2001 Increased damage from fires in logged forests during droughts caused by El Niño. *Nature* **414**, 437–440.
- Thompson, A. M., Witte, J. C., Hudson, R. D., Guo, H., Herman, J. R. & Fujiwara, M. 2001 Tropical tropospheric ozone and biomass burning. *Science* **291**, 2128–2132.
- Trenberth, K. E. 2002 Changes in tropical clouds and radiation. *Science* **296**, 2095a–2095a.
- Waring, R. H. & Pitman, G. B. 1985 Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* **66**, 889–897.
- White, A., Cannell, M. G. R. & Friend, A. D. 2000 CO₂ stabilization, climate change and the terrestrial carbon sink. *Global Change Biol.* **6**, 817–833.
- Wielicki, B. A. (and 12 others) 2002 Evidence for large decadal variability in the tropical mean radiative energy budget. *Science* **295**, 841–844.
- Williamson, G. B., Laurance, W. F., Oliveira, A. A., Delamonica, P., Gascon, C., Lovejoy, T. E. & Pohl, L. 2001 Amazonian tree mortality during the 1997 El Niño drought. *Conserv. Biol.* **14**, 1538–1542.
- Woodwell, G. M. 1986 Forests and climate: surprises in store. *Oceanus* **29**, 71–75.
- Woodwell, G. M. 1995 Biotic feedbacks from the warming of the earth. In *Biotic feedbacks in the global climatic system: will the warming feed the warming?* (ed. G. M. Woodwell & F. T. Mackenzie), pp. 3–21. Oxford University Press.
- Wurth, M. K. R., Winter, K. & Korner, C. 1998a Leaf carbohydrate responses to CO₂ enrichment at the top of a tropical forest. *Oecologia* **116**, 18–25.
- Wurth, M. K. R., Winter, K. & Korner, C. 1998b *In situ* responses to elevated CO₂ in tropical forest understorey plants. *Funct. Ecol.* **12**, 886–895.
- Yokouchi, Y., Ikeda, M., Inuzuka, Y. & Yukawa, T. 2002 Strong emission of methyl chloride from tropical plants. *Nature* **416**, 163–165.
- Zhang, H., Henderson-Sellers, A. & McGuffie, K. 2001 The compounding effects of tropical deforestation and greenhouse warming on climate. *Climate Change* **49**, 309–338.
- Zotz, G. & Winter, K. 1996 Diel patterns of CO₂ exchange in rainforest canopy plants. In *Tropical forest plant ecophysiology* (ed. S. S. Mulkey, R. L. Chazdon & A. P. Smith), pp. 89–113. New York: Chapman & Hall.

GLOSSARY

- BVOC: biogenic volatile organic compound
 CO₂: carbon dioxide
 [CO₂]: carbon dioxide concentration
 ENSO: El Niño-Southern Oscillation
 GPP: gross primary productivity
 NEE: net ecosystem exchange of CO₂
 NPP: net primary productivity
 OTS: Organization for Tropical Studies
 TNC: total non-structural carbohydrate