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Fingerprinting the impacts of global change on tropical forests

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Recent observations of widespread changes in mature tropical forests such as increasing tree growth, recruitment and mortality rates and increasing above-ground biomass suggest that 'global change' agents may be causing predictable changes in tropical forests. However, consensus over both the robustness of these changes and the environmental drivers that may be causing them is yet to emerge. This paper focuses on the second part of this debate. We review (i) the evidence that the physical, chemical and biological environment that tropical trees grow in has been altered over recent decades across large areas of the tropics, and (ii) the theoretical, experimental and observational evidence regarding the most likely effects of each of these changes on tropical forests. Ten potential widespread drivers of environmental change were identified: temperature, precipitation, solar radiation, climatic extremes (including El Niño–Southern Oscillation events), atmospheric CO₂ concentrations, nutrient deposition, O₃/acid depositions, hunting, land-use change and increasing liana numbers. We note that each of these environmental changes is expected to leave a unique 'fingerprint' in tropical forests, as drivers directly force different processes, have different distributions in space and time and may affect some forests more than others (e.g. depending on soil fertility). Thus, in the third part of the paper we present testable *a priori* predictions of forest responses to assist ecologists in attributing particular changes in forests to particular causes across multiple datasets. Finally, we discuss how these drivers may change in the future and the possible consequences for tropical forests.

Keywords: review; carbon; permanent sample plot; forest dynamics; mortality; recruitment

1. INTRODUCTION

Over the past century virtually all ecosystems on Earth have come under increasing human influence. This has been through direct contact and transformation (e.g. for farming, through hunting or the use of fire), the effects of habitat fragmentation, the production of pollutants (e.g. tropospheric O₃) or the substantial alteration of major biogeochemical cycles, such as the global C, water and N cycles (Vitousek *et al.* 1997; Fowler *et al.* 1999; Prentice *et al.* 2001; Ramanathan *et al.* 2001; Galloway *et al.* 2002; Barlow & Peres 2004; Laurance 2004; Malhi & Wright 2004). However, for tropical forests that are far from most direct human impacts, the question as to whether these ecosystems have been substantially altered and what may be causing these changes is actively debated (Clark 2004; Chambers & Silver 2004; Lewis *et al.* 2004; Phillips *et al.* 2004).

Whether tropical forests are showing widespread secular changes in dynamics, and why, is of broad interest as tropical forests store *ca.* 40% of the C residing in terrestrial vegetation and annually process about six times as much C through photosynthesis as humans release to the atmosphere through fossil fuel combustion (Malhi &

Grace 2000; Malhi *et al.* 2002a). In addition, tropical forests harbour more than 50% of the world's species (Heywood 1995). Thus, relatively small yet consistent changes *within* remaining tropical forests as a biome could have global consequences for the climate, biodiversity, the global C cycle, the rate of climate change and hence human welfare.

Two widespread changes in tropical forests have received attention: increases in tree stem turnover and increases in the above-ground biomass of forest stands (Phillips & Gentry 1994; Phillips *et al.* 1998). A case can be made that these trends have not been caused by widespread changes in environmental drivers, but are the product of compilations of disparate datasets containing methodological errors coupled with the use of inappropriate statistical techniques (Sheil 1995; Sheil & May 1996; Condit 1997; Clark 2002). In response, much work has gone into expanding the datasets, particularly across South America (Malhi *et al.* 2002b), and addressing these 'artefactual' explanations of the trends (Phillips 1995, 1996; Phillips *et al.* 2002a, 2004; Baker *et al.* 2004; Lewis *et al.* 2004). These newer analyses confirm the qualitative findings of the initial two analyses, and have shown additional trends in South American tropical forests:

- (i) that stem turnover is rising owing to simultaneous increases in both recruitment and mortality;
- (ii) that recruitment rates are greater than mortality rates, causing a net increase in stem density;

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

- (iii) that stand-level growth and mortality, in terms of biomass, have both increased; and
- (iv) that growth rates are greater than mortality rates, leading to the documented increase in above-ground biomass (Baker *et al.* 2004; Lewis *et al.* 2004; Phillips *et al.* 2004).

Thus, one obvious question is: what may be causing such a suite of changes across large areas of tropical forest? To answer this question we first need to know which physical, chemical and biological changes to the environment have occurred over recent decades and what their likely effects on tropical forest trees have been. Thus, in this paper, we systematically review the evidence that various widespread environmental changes have occurred across the tropics and assess the evidence of the most likely effects of each of these changes on tropical forests.

Confidently attributing widespread changes in tropical forests to particular causal mechanisms is difficult. The problem is rooted in the fact that realistic experiments are virtually impossible owing to physical, financial and ethical constraints. For example, realistic experiments on natural stands of tropical trees by raising atmospheric CO₂ levels from pre-industrial levels upwards are impossible as no existing forests are acclimated to pre-industrial CO₂ levels. Furthermore, direct tests of whether the loss of large mammals is changing forest ecology are not possible as in many cases the large mammals are endangered species. Thus, many studies must be essentially correlational, for example, monitoring forest plots over time and noting that biomass has increased simultaneously with atmospheric CO₂ concentrations. Causation is assigned by inference, by necessity from somewhat unrealistic experiments, such as growing tropical tree seedlings in pots under current and higher CO₂ concentrations. Overall, because the correlation-experimental inference-causation process is open to debate at all stages, generally accepted causes of changes in tropical forests have so far remained elusive. An example of this has been the ongoing debate over apparent biomass increases in tropical forests and what may be causing them (Phillips *et al.* 1998, 2002a; Clark 2002, 2004; Nemani *et al.* 2003; Baker *et al.* 2004; Chambers & Silver 2004; Lewis *et al.* 2004). Hence, here we develop an approach to narrow the range of potential causal agents that may be altering tropical forests, by formalizing the procedure of attributing particular changes to particular causes within a consistent framework.

2. GENERAL FRAMEWORK

We propose a framework that consists of four parts:

- (i) a systematic identification of possible mechanisms that may cause change;
- (ii) an assessment of how much each potential driver has changed over the late twentieth century;
- (iii) an assessment of whether the level of change in the driver is likely to be ecologically meaningful; and
- (iv) use of the knowledge that the different types of environmental change directly force different ecological processes, have varying distributions in space and time, and may affect some forests more than others (e.g. depending upon soil fertility), to

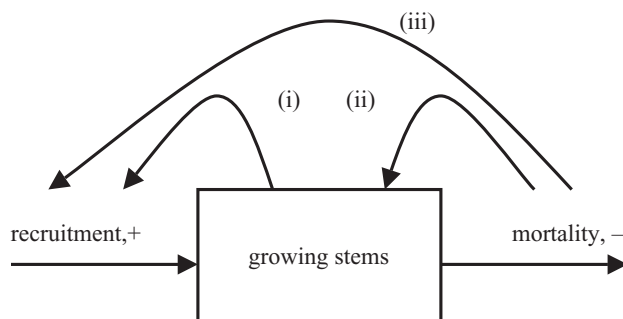


Figure 1. Schematic diagram of the relationships between stem mortality, recruitment and growth of stems in a forest stand. Recruitment adds and mortality subtracts (the fluxes) stems from the standing stock of growing stems in the stand (the pool). The processes are linked as (i) growth affects recruitment, as a change in growth will change the rate of arrival of stems at the minimum threshold to join the stem population, (ii) mortality affects growth, as changes in mortality change the number of remaining stems altering competition for resources, and (iii) mortality affects recruitment, through the same process as (ii). The system is time lagged: a change to either growth, recruitment or mortality will take time to percolate through the system, for example, an increase in mortality will not cause an instantaneous increase in recruitment, as stems will take time to respond and grow to become newly recruited stems. The same applies to biomass: a pool (standing stock) and input (growth increments) and output (losses of biomass from mortality) fluxes are also linked in a time-lagged circular process.

generate unique *a priori* predictions for each hypothesized change.

In the future, new hypotheses can be added to the framework, or refinements made to existing hypotheses and predictions, as necessary.

This paper follows the same structure as the framework, where we first identify drivers and report best estimates of how much they have changed over recent decades, and second develop a comparative review of the theoretical, experimental and observational evidence that changes in a given driver may cause changes in tropical forests. Given the lack of experiments documenting responses of mature old-growth tropical forest stands to rising air temperatures, CO₂, N depositions and other potential drivers, this section is by necessity somewhat speculative; thus, predictions are likely to be altered and refined in the future. Finally, we make unique *a priori* predictions, or fingerprints, of changes in growth, recruitment or mortality in forests in response to changes in the environmental drivers that were identified.

For the purposes of identifying possible mechanisms of change, we assume that tropical tree populations are in a three-phase, time-lagged circular system that links growth, recruitment and mortality processes (figure 1). Changes in these process rates result from forcing one of these processes, which in turn may alter the other two processes. To generate potential drivers of change we review the literature focusing on each process in turn (growth, recruitment, mortality), systematically considering physical, chemical and biological drivers of change. We consider all potential drivers of change, regardless of

whether they may be caused by anthropogenic changes or decadal-scale environmental oscillations, as are known to occur, particularly in the climate system (Botta *et al.* 2002; Wielicki *et al.* 2002). We do not include an exhaustive list of possible drivers, if they appear very implausible. For example, small decreases in stratospheric O₃, and hence increases in UV-B radiation, may or may not have occurred over tropical latitudes (Madronich & de Gruijl 1993; Staehelin *et al.* 2001), and in any case would have probably had only very small effects on tropical plants (Searles *et al.* 1995; Ziska 1996).

3. ENVIRONMENTAL CHANGES OVER THE PAST THREE DECADES

We identified four potential physical drivers of change: air temperatures, precipitation, solar radiation and climatic extremes (including ENSO); three potential chemical drivers: atmospheric CO₂ concentrations, nutrient depositions and tropospheric O₃/acid deposition; and one potential biological driver: hunting pressure (table 1). Two further drivers were identified: first, land-use changes that can simultaneously alter the physical, chemical and biological environment, and second, increases in lianas (woody climbing plants) of which the cause is unknown. Altogether we identified 10 distinct drivers. Only one of these drivers, changes in hunting pressure, is expected to initially drive changes in tree recruitment (table 1). Both changes in climatic extremes/ENSO events and increasing liana density are expected to initially drive changes in mortality. Land-use changes are expected to change both recruitment and mortality via different mechanisms. The other seven drivers are all expected to initially drive changes in tree growth.

Having identified 10 possible drivers, we describe how much each driver has changed across the tropical forest biome. We also want to compare the rates of change in each driver. However, the quality of the data varies widely, and is frequently very sparse both spatially and temporally. Indeed, we are often making the first estimate of changes over the biome. Therefore, we have attempted to standardize these disparate datasets, by

- (i) reporting the published magnitudes of change for each driver in the main body of the text;
- (ii) selecting a 20 year time-series, if available, closest to 1980–2000, and using linear regression to estimate rates of changes (table 1); and
- (iii) presenting annualized data from 1970 to 2000, where available, to allow visual comparisons between different drivers (figure 2). The 1970–2000 period corresponds to most contemporaneous forest monitoring data; the period 1980–2000 corresponds to the best available driver data for the greatest number of drivers.

The reader should note several further points when interpreting the time-series data for drivers. First, the number and location of monitoring stations contributing data sometimes change through time (e.g. rainfall, temperature, solar radiation). Second, uncertainties are associated with some measurements (e.g. solar radiation). Third, strong spatial variability may contribute to observed trends

(e.g. rainfall). Fourth, different studies often have differing definitions of ‘tropical forest’, which further complicate comparisons. Below, each section reports the changes of a given driver across the tropical forest biome over the past three decades.

(a) *Temperature*

Global land surface temperatures have increased by 0.6 °C over the past century (IPCC 2001). This has largely been caused by the production of greenhouse gases, such as CO₂ from fossil fuel combustion (IPCC 2001). Over the past two decades there has been a 0.26 ± 0.05 °C per decade increase in air temperatures over the tropical forest biome (figure 2; Malhi & Wright 2004). The increase in daily minimum (night-time) temperatures has been much greater than the increase in daily maximum temperatures (IPCC 2001). These temperature increases are consistent with the effects of the radiative forcing of the increased concentrations of greenhouse gases in the atmosphere. The warming appears consistent and widespread across almost all tropical regions, although in some regions local climatic oscillations diminish or enhance the warming (IPCC 2001; Malhi & Wright 2004). Linear regression of the mean annual air temperature and calendar year between 1978 and 1998 gives a mean change of 0.024 °C yr⁻¹ (figure 2; table 1). Increasing temperatures are expected to rise across tropical regions by an additional 2–5 °C over the next century (Hulme & Viner 1998; Cox *et al.* 2000; IPCC 2001; Zhang *et al.* 2001).

(b) *Precipitation*

Globally, rainfall has increased in response to climate change (IPCC 2001; New *et al.* 2001). However, across the tropics, land surface measurements show a decrease in rainfall over the twentieth century, but with little trend over recent decades (IPCC 2001). Within the tropical forest biome there has been a pan-tropical decrease in rainfall from the mid-1970s, by 22 ± 17 mm per decade or 1% per decade (figure 2; Malhi & Wright 2004). However, this global trend is mainly caused by a strong and significant decline in rainfall in the northern African tropics ($-2.4 \pm 1.3\%$ per decade), with no significant trend in other tropical forest regions (Malhi & Wright 2004). Similarly, the strength and intensity of the dry season have increased pan-tropically (figure 2), but this is again caused by a significant increase in Africa but not in Latin America or Asia (Malhi & Wright 2004). These regional-scale changes in rainfall patterns may be caused by long-term oscillations and/or responses to increases in anthropogenic aerosols (Ramanathan *et al.* 2001; Allen & Ingram 2002; Kaufman *et al.* 2002). A linear regression of mean annual rainfall for the entire tropical forest region from 1978 to 1998 reveals a decrease in rainfall across the biome of -0.067 mm yr⁻¹ (table 1; figure 2), driven by decreases in Africa alone.

(c) *Solar radiation*

The amount of incoming solar radiation may have increased over much of the tropics over the past two decades, owing to a decrease in tropical cloudiness as measured by satellite data measuring the TOA tropical radiative energy budget (Chen *et al.* 2002; Wielicki *et al.*

Table 1. Summary of changes in the physical, chemical and biological environment that may be driving temporal changes in the structure and dynamics of the tropical forest biome.

driver	hypothesis	description of mechanism	level of driver	impact of driver	scale of change ^a	type of change ^b	extent of change ^c	absolute annual change ^d	theoretical consistency of effects? ^e	mechanism experimentally demonstrated?	key prediction
1. air temperature	air temperature	long-term temperature increases affect photosynthesis, increasing/decreasing growth rates	physical	growth	regional	point	global	+0.024 °C	no	yes	growth rate changes correlate with local temperature trends
2. air temperature	respiration costs	long-term temperature increases increase respiration rates, decreasing growth rates	physical	growth	regional	point	global	+0.024 °C	yes	yes	growth rate changes correlate with increases of minimum temperatures
3. air temperature	soil warming	long-term temperature increases increase soil nutrient availability, increasing or decreasing growth rates	physical	growth	regional	point	global	+0.024 °C	no	partly ^f	growth rate changes correlate with local temperature trends, with highest relative increases on nutrient-poor soils
4. rainfall	rainfall	long-term rainfall changes affect growth where water is a limiting resource	physical	growth	regional	point	regional	-0.067 mm	yes	yes	only water-limited sites where rainfall has decreased show dynamics change
5. solar radiation	global dimming	long-term decreases in insolation affect photosynthesis, increasing/decreasing growth rates	physical	growth	regional	point	regional/ near-global	-0.30 W m ⁻²	no	partly ^f	growth rate changes correlate with local insolation trends
6. solar radiation	changing energy budget	recent increases in solar radiation owing to decreased cloudiness increase growth rates	physical	growth	regional	point	regional	+0.13 W m ⁻²	yes	yes	growth rate changes correlate with local insolation trends
7. climatic extremes/ ENSO	climatic extremes/ ENSO	increased frequency and/or severity of extreme weather events increases tree mortality	physical	mortality	local/ regional	point + extension	regional/ near-global	-0.020 index units	yes	yes	dynamics altered where extremes, e.g. ENSO drought, are known or suspected to have occurred
8. CO ₂	light-use efficiency	long-term atmospheric CO ₂ increases increase photosynthesis, increasing growth rates	chemical	growth	global	point	global	+1.53 p.p.m.	yes	yes	growth rate increases across most forests, with greatest absolute increase in nutrient-rich aseasonal forests
9. CO ₂	water-use efficiency	long-term atmospheric CO ₂ increases increase water-use efficiency, increasing growth where water is a limiting resource	chemical	growth	global	point	regional/ near-global	+1.53 p.p.m.	yes	yes	growth rate increases at nutrient-rich seasonal sites even where no change in rainfall

(Continued.)

Table 1. (Continued.)

driver	hypothesis	description of mechanism	level of driver	impact of driver	scale of change ^a	type of change ^b	extent of change ^c	absolute annual change ^d	theoretical consistency of effects? ^e	mechanism experimentally demonstrated?	key prediction
10. nutrient depositions	N deposition	changes in N-deposition change growth rates	chemical	growth	regional	extension + some point	regional	+0.013 kg N ha ⁻¹	yes ^g	yes ^g	changes in growth rates where deposition has increased
11. nutrient depositions	P deposition	changes in P-deposition change growth rates	chemical	growth	regional	extension + some point	regional	unquantified	yes ^g	yes ^g	changes in growth rates where deposition has increased
12. O ₃ /acid deposition	O ₃ /acid deposition	increases in acidity of rainfall and tropospheric ozone decrease growth and increase mortality	chemical	growth	regional	extension + some point	regional	+1.1 million ha > 60 p.p.b. O ₃	yes	yes	changes where changes in driver known or suspected to occur, e.g. downwind of biomass burning/industrial activity
13. hunting	competitive release	hunting of frugivores impacts seed dispersal of large-seeded species, benefiting small-seeded animal- and wind-dispersed seeds which have higher growth and stem turnover rates	biological	recruitment	local	extension, point	near global	+0.13 million tonnes bushmeat	yes	no	only defaunated sites would show changes
14. land-use change	edge effects	tree mortality increases owing to increasing encroachment of human-modified habitat	biological	mortality	local	extension	near global	unquantified increase	yes	yes	mortality increases correlated with distance from edge
15. land-use change	fragmentation-pioneer effects	habitat fragmentation increases the number of pioneer trees in degraded areas which flood remaining forest with their seed, increasing pioneer numbers, increasing recruitment	biological	recruitment	local	extension	near global	+0.59 million ha	yes	no	disregarding pioneer species from data removes effects

(Continued.)

Table 1. (Continued.)

driver	hypothesis	description of mechanism	level of driver	impact of driver	scale of change ^a	type of change ^b	extent of change ^c	absolute annual change ^d	theoretical consistency of effects? ^e	mechanism experimentally demonstrated?	key prediction
16. second-order	lianas	tree mortality increases owing to increased liana loading	biological	mortality	unknown ^h	unknown ^h	unknown ^h	+0.28 lianas ha ⁻¹	yes	no	mortality increases where significant increases in liana populations detected or suspected

^a Scale at which changes are relatively uniform (local, regional, global).

^b Either a driver increases by Y at a point X where it was initially absent (extension changes), or a driver increases by Y at a point X where it was initially present (point change).

^c Product of scale at which changes are relatively uniform and the extent of those changes (regional, near global, global).

^d Using linear regression on available annual means for each driver from 1980 to 2000, where possible.

^e Is there consensus in the published literature that if a driver changes the process driven will occur in a specified direction?

^f Shown for a temperate forest.

^g Addition of nutrients increases growth if that nutrient is limiting; but which nutrient is limiting is unknown in most forests.

^h Depends on driver of increases in lianas.

2002). The satellites measure LW radiation emitted back to space, which is related to cloudiness. From 1979 to the mid-1980s there was a decrease in LW radiation of *ca.* 2 W m^{-2} , followed by an increase of *ca.* 6 W m^{-2} from a background rate of *ca.* 247 W m^{-2} , indicating that the tropics has become less cloudy and hence sunnier (Wielicki *et al.* 2002). Chen *et al.* (2002) show LW radiation increases over the tropics of 3.7 W m^{-2} per decade from 1985 to 2001 using a similar dataset. Using linear regression on annual estimates of LW radiation from Wielicki *et al.* (2002) from 1981 to 2001, LW radiation increased by $0.13 \text{ W m}^{-2} \text{ yr}^{-1}$ (figure 2; table 1). It is suspected that these changes are caused by natural decadal-scale oscillations and are not direct responses to anthropogenic climate change; thus, recent increases are not expected to persist (Wielicki *et al.* 2002).

By contrast, ground-based measurements from thermopile pyranometers suggest that significant reductions in solar radiation reaching the Earth's surface have occurred during the past 50 years, termed 'global dimming' (Stanhill & Cohen 2001). Globally, the reduction has been estimated to be *ca.* 2.7% per decade or $0.51 \pm 0.05 \text{ W m}^{-2} \text{ yr}^{-1}$. The values for the northern and southern tropics are -0.38 and $-0.65 \text{ W m}^{-2} \text{ yr}^{-1}$, respectively. Stanhill & Cohen (2001) suggest that the reduction in solar radiation is most probably caused by anthropogenic aerosols that have altered the optical properties of the atmosphere. Aerosols have increased globally over recent decades, including across much of the tropics (Ramanathan *et al.* 2001; Kaufman *et al.* 2002). Indeed, in regions close to deforestation zones (e.g. Rondonia in Brazil, much of Southeast Asia), the presence of a dry-season burning haze is well documented, and can reduce solar radiation reaching the land surface by more than 15% (Eck *et al.* 1998). In figure 2 we report the temporal trend from the Southern Hemisphere data in Stanhill & Cohen (2001) as this is more likely to mirror the tropical trend than the Northern Hemisphere, which has larger industrialized areas than either the Southern Hemisphere or the tropics. This shows no change in incoming solar radiation from 1952 to 1988 followed by a steep decline in 1992 (figure 2). Using linear regression, the solar radiation data spanning 1970–1992 from the Southern Hemisphere show a reduction of $0.3 \text{ W m}^{-2} \text{ yr}^{-1}$.

How can there be evidence of increases and decreases in solar radiation? The contrasting data are difficult to reconcile. One or both sets of measurements may contain hidden biases especially as both patterns are new data compilations and analyses. We suggest three possible explanations that do not invoke measurement error or bias. First, the global dimming paper compares the years 1958, 1965, 1975, 1985 and 1992 (Stanhill & Cohen 2001), whereas the satellite TOA data cover 1979–2001 (Wielicki *et al.* 2002). The TOA measurements show very large variations, and comparing 1985 and 1992—the years covered by both sets of measurements—the two datasets are in qualitative agreement, both showing a decline in solar radiation. Second, Nemani *et al.* (2003) use the TOA satellite data and show that average increases in solar radiation across the tropics are dominated by increases across Amazonia, whereas none of the measurements from the global dimming compilation is from Amazonia (which is dominated by sensors located in Asia). Hence, an increase

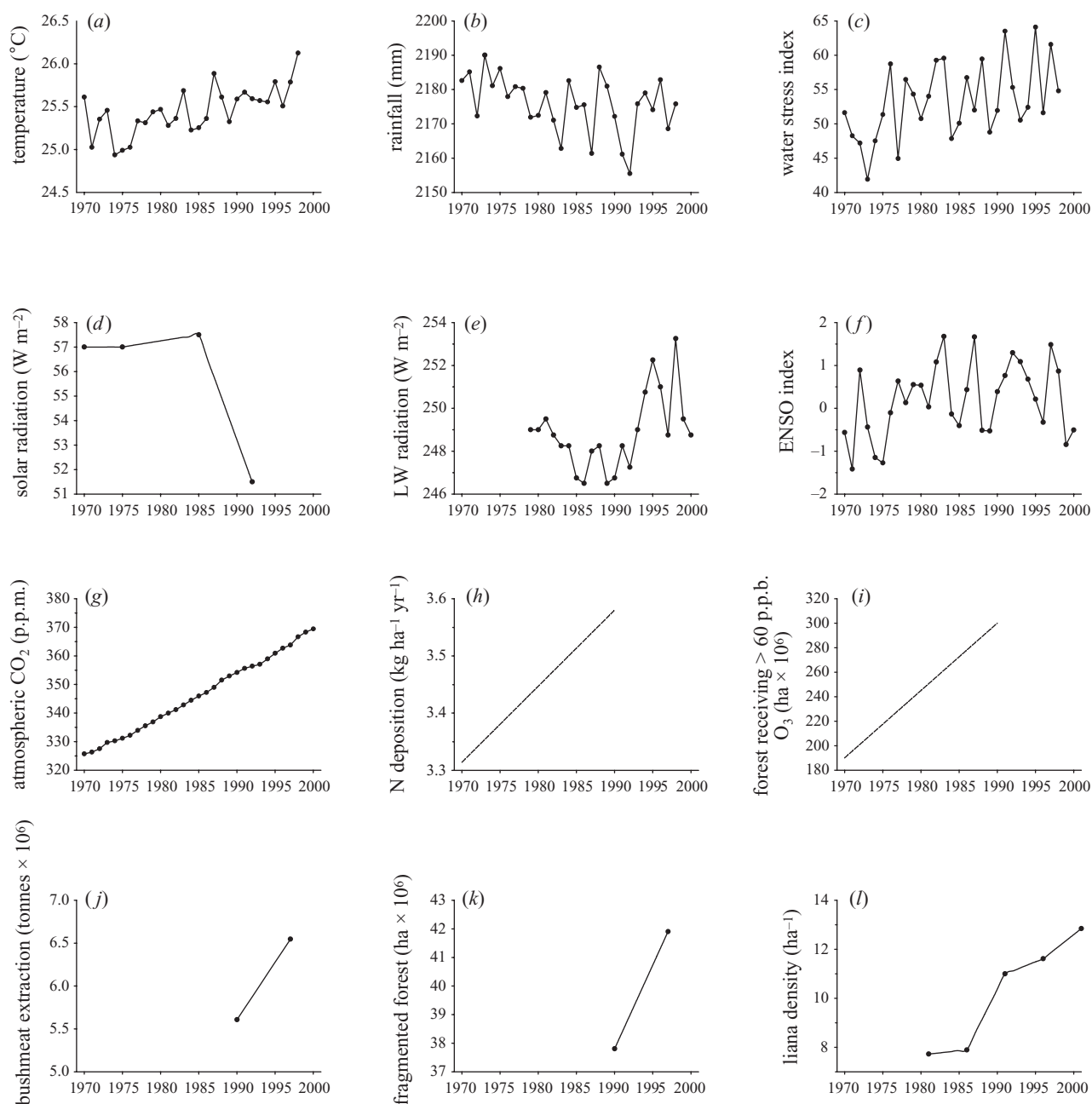


Figure 2. Environmental changes across the tropical forest biome, 1970–2000. Dots represent data points, solid lines are linear interpolation between data points. Dashed lines represent linear regression from numerical model output. The data are from multiple sources and are extremely variable. Cautious interpretation is required; see § 3 for details. Data represent mean changes for the biome unless otherwise stated. (a) Mean annual air temperature, (b) mean annual rainfall (note: most regions show no trend; the decline is driven largely by one area, northern Congo), (c) the water stress index of Malhi & Wright (2004) (note: most regions show no trend; the decline is driven largely by one area, northern Congo), (d) total solar radiation from ground measurements from across the Southern Hemisphere, (e) estimated annual TOA LW radiation, correlated with cloudiness and hence incoming solar radiation, from 20° N to 20° S, (f) annual multivariate ENSO index anomaly, (g) annual atmospheric CO₂ concentration measured at Mauna Loa, Hawai'i, (h) estimated mean annual average N deposition onto tropical forests, from model output, (i) estimated amount of forest receiving high O₃ depositions, from model output, (j) estimated total wild mammal meat extraction from tropical forests, (k) total tropical forest in small fragments, estimated from satellite data, (l) large (more than 10 cm diameter) liana density in western Amazonian forest plots.

in solar radiation may be occurring in Amazonia, while a decrease may be occurring across much of Southeast Asia. This could reconcile both sets of measurements. Third, Mt Pinatubo erupted in 1991, and by 1992 reduced solar radiation globally (Gu *et al.* 2003). In the global dimming dataset, the data from the Southern Hemisphere show no reduction in solar radiation over time, except in 1992, which has very low solar radiation measurements (figure

2). Thus, while the trend in the industrialized Northern Hemisphere may be long term and caused by human activities, the Southern Hemisphere, and hence perhaps most of the tropics, may not be showing a trend, but merely reflecting the transient conditions following the 1991 Mt Pinatubo eruption. Overall, changes in solar radiation and alterations in diffuse/direct components remain open to debate.

(d) Climatic extremes|El Niño–Southern Oscillation

Climatic extremes across much of the tropics are strongly correlated with ENSO events, a quasi-regular internal oscillation of the equatorial Pacific ocean and the atmosphere (Trenberth 1997; Fedorov & Philander 2000). The El Niño (positive) phase of an ENSO event can cause widespread intense drought across many, but not all, tropical areas, whereas its complementary La Niña (negative) phase can cause very heavy rainfall and flooding in these areas. The regions where precipitation is most affected by ENSO extremes are northern-eastern Amazonia, Central America and insular Southeast Asia, whereas precipitation in African tropical forests shows little consistent relationship with ENSO events (Malhi & Wright 2004). Some dry margins of the tropical forest belt are anti-correlated with ENSO, with increased rainfall during El Niño events. Almost all tropical regions experience higher temperatures during the El Niño phase, independent of any change in rainfall (Malhi & Wright 2004).

There is some evidence that the number, duration and intensity of ENSO events have increased over the twentieth century, but it is unclear as to what extent this may represent longer-term internal oscillations in ENSO magnitude (Tudhope *et al.* 2001). Over the past 30 years there has been little discernible trend (figure 2). However, two of the strongest ENSO events in the twentieth century occurred in the past two decades, in 1982–1983 and 1997–1998. More generally, extreme climatic events such as droughts, including ENSO droughts, windstorms and intense rainfall events, are likely to increase as a result of climate change (IPCC 2001). However, such events are inherently sporadic and increases have not been documented to date (IPCC 2001). Using annual measurements of the multivariate ENSO Index from 1978 to 1998 and linear regression actually reveals a small *decrease* in ENSO strength of -0.02 index units yr^{-1} between 1980 and 2000 (table 1; figure 2).

(e) Carbon dioxide

Concentrations of CO_2 in the atmosphere have increased over the past 150 years as a result of fossil fuel combustion and deforestation. At the time of the Industrial Revolution levels were *ca.* 280 p.p.m. rising to *ca.* 370 p.p.m. in 2002. From 1980 to 2000 the annual increase has been *ca.* 1.53 p.p.m. or 0.45% yr^{-1} (figure 2; Prentice *et al.* 2001). This change has occurred fairly steadily and uniformly globally, although plants experience diurnal and seasonal changes in CO_2 concentrations (Prentice *et al.* 2001; Ziska *et al.* 2001). Current levels are already the highest for *ca.* 20 million years and within this century may reach levels unprecedented since the Early Eocene (Royer *et al.* 2001). Increases are expected to continue over the coming century, the rate of which will depend on the amount of fossil fuels burnt, deforestation rates and feedbacks between the climate system and the biosphere (Cox *et al.* 2000; IPCC 2001).

(f) Nutrient depositions

Globally, human activities have more than doubled inputs of N, as both oxidized N compounds, NO_x , and the reduced N compound, NH_3 , to terrestrial ecosystems (Holland *et al.* 1999; Galloway *et al.* 2002). While most

of these increases have been in temperate regions (owing to most sources being at mid-latitudes and the short life-span of NO_x and NH_3 in the atmosphere), N deposition rates have increased substantially across the tropics over recent decades, caused by increases in fertilizer use, fossil-fuel combustion and biomass burning (Galloway *et al.* 1994; Matson *et al.* 1999, 2002). Increases in fertilizer and fossil fuel use have been marked over much of Central America, Brazil's Atlantic Coast and much of Asia (Galloway *et al.* 2002). Meanwhile, increases in biomass burning have occurred in eastern and southern Amazonia and across much of Asia. It is estimated, using data on N sources and an atmospheric transport model, that N deposition from both NO_x and NH_3 has increased from *ca.* 1.9 $\text{kg N ha}^{-1} \text{yr}^{-1}$ before the Industrial Revolution to 3.6 $\text{kg N ha}^{-1} \text{yr}^{-1}$ in the 1990s across the tropical forest biome (Holland *et al.* 1999). Assuming a linear increase from 1860 to 1990, the annual rate of increase would be 0.013 $\text{kg N ha}^{-1} \text{yr}^{-1}$ (figure 2; table 1). A further increase in the extent and load of N deposition is expected in the future as biomass burning continues, and industrialization and more intensive farming spread further across the tropics. It is likely that deposition of other nutrients, notably P, may have also increased near biomass-burning sites (Artaxo *et al.* 2002), but global-scale estimates of increases in P and other nutrient depositions are, to our knowledge, unavailable.

(g) Ozone|acidic depositions

Increasing industrialization, intensive agricultural activity and biomass burning produce various atmospheric pollutants that form the photochemical oxidant O_3 , which may damage plants (Chameides *et al.* 1994; McLaughlin & Downing 1995; Fowler *et al.* 1999; Kita *et al.* 2000; Emberson *et al.* 2001). It has been estimated, using data on known O_3 sources and an atmospheric transport model, that in 1860 no tropical forest exceeded 60 p.p.b. of O_3 exposure (considered a threshold for O_3 that is known to cause damage to some plants under some conditions). This threshold was exceeded within an area of 1.9 million km^2 of tropical forest by 1970 and by an area of 3.0 million km^2 of forest in 1990, or 0%, 12.1% and 19.1% of the total tropical forest cover, respectively (Fowler *et al.* 1999). Assuming a linear increase between 1970 and 1990, this is an increase in forest exposed to more than 60 p.p.b. O_3 of 5.5 million ha yr^{-1} . The increase has been particularly great across Southeast Asia compared with Africa or South America (Fowler *et al.* 1999). As industrialization and more intensive agriculture spread across tropical regions, the size of affected areas and quantity of exposure are expected to increase.

The same processes that produce O_3 also produce pollutants such as SO_2 , which causes acid rain (as do N depositions) and can also damage plants (Chameides *et al.* 1994; Fowler *et al.* 1999; Emberson *et al.* 2001; Potter *et al.* 2002). Again, Southeast Asia is the most affected area: as a region, it emits more SO_2 into the atmosphere than does either Europe or North America (Galloway & Rodhe 1990). The affected areas are likely to be those that are also affected by N deposition, as there are good correlations between O_3 exposure and N deposition (Ollinger *et al.* 2002).

(h) Hunting

Hunting of wild mammal meat (bushmeat) is the single most geographically widespread form of resource extraction in tropical forests, affecting even remote areas of forest (Woodroffe & Ginsberg 1998; Robinson & Bennett 2000; Fa *et al.* 2002). Access routes penetrate most surviving forest; for example, only 20% of Brazilian Amazonian forest is more than 9 km from the nearest navigable river or a road (Peres & Lake 2003). The total amount of bushmeat extracted may exceed 5 million tonnes annually (Fa *et al.* 2002). It has been estimated that bushmeat extraction rates have increased in recent years owing to increased access to previously inaccessible forest, increasingly widespread use of more efficient hunting technology, rising human populations, increasing integration of subsistence hunters into local, national and international markets, and because in many places bushmeat is a preferred food (Robinson & Bennett 2000).

We do not know of a published pan-tropical estimate for the increase in hunting pressure. We know that increasing hunting pressure follows forest accessibility, usually logging (Peres & Lake 2003), and that newly accessible areas have extraction rates of between three and six times those of nearby inaccessible areas (Robinson *et al.* 1999). Thus, we can make an initial estimate of changes in hunting pressure on the basis of

- (i) bushmeat extraction rates;
- (ii) the amount of forest cover;
- (iii) the area of forest degraded annually; and
- (iv) rates of extraction in newly accessible areas.

We use extraction data from the Amazon and Congo Basins (Fa *et al.* 2002). We assume that Southeast Asia has similar extraction rates to Amazonia (which may be conservative). We then assume that bushmeat extraction increases only in degraded forest (mostly caused by logging), and that newly degraded forest has an extraction rate of four times the average (Robinson *et al.* 1999). We use forest cover and degraded-area estimates from 1990 and 1997 reported by Achard *et al.* (2002). Thus, four times the average extraction rate multiplied by the annual area degraded gives an approximate annual increase in hunting pressure. Finally, we add the extra extraction from population growth, at 1.6% yr⁻¹ for developing countries (Cincotta *et al.* 2000). Based on these calculations, we estimate that hunting pressure increased from *ca.* 5.6 million tonnes of wild meat per annum in 1990 to *ca.* 6.5 million tonnes per annum in 1997, an increase of *ca.* 130 000 tonnes of wild meat per annum (table 1; figure 2). Most of the increase in absolute terms occurred in Africa, because initial extraction rates there were much higher than in Latin America. In relative terms, Southeast Asia shows the greatest increase, as annually more forest was made accessible there. These figures are a first estimate. They are likely to underestimate the increase, as

- (i) the forest degradation and loss data we use may be very conservative (cf. FAO 2000);
- (ii) no changes in hunting technology are included in the calculations; and
- (iii) the population-increase estimates we use are probably underestimates (Cincotta *et al.* 2000).

(i) Land-use change

Across the tropics between 6 and 14 million ha of tropical forest are destroyed annually, the differences being due to different definitions of tropical forest and the methodologies used (FAO 2000; Achard *et al.* 2002; DeFries *et al.* 2002). DeFries *et al.* (2002), using satellite images, show an increase in deforestation of *ca.* 10% from the 1980s to the 1990s, caused by a large increase in forest clearing across Asia. By contrast, FAO assessments, using a variety of sources, show no significant changes in deforestation rates from the 1980s to the 1990s. Furthermore the FAO estimates of deforestation across both the 1980s and 1990s are much higher than the exclusively satellite-based estimates by DeFries *et al.* (2002) and Achard *et al.* (2002).

The wide differences in forest-loss rates are likely to be caused by differing definitions of 'tropical forest' and 'deforestation' coupled with the relative contributions of either satellite images (which can be difficult to interpret) and country reports (which can sometimes be unreliable). Satellite images can often present difficulties in detecting forest loss when new vegetation rapidly replaces deforested land, which may then be difficult to distinguish from mature forest in the image. Thus, while satellite studies are good at quantifying *net* changes in forest cover, they may be less effective for quantifying deforestation *per se*, and are likely to underestimate deforestation rates.

Regardless of the actual numbers involved, the remaining forest is inevitably fragmented (Skole & Tucker 1993). The process can be either highly localized in some regions, as is the case in central Amazonia, or very widespread, as is the case in eastern and southern Amazonia and much of Southeast Asia. However, fragmentation is occurring globally (McCloskey 1993; Achard *et al.* 2002). The process of land clearance often begins with logging. Estimates are that 58%, 19% and 28% of Asian, African and Latin American tropical forests, respectively, were already commercially logged by the mid-1990s (Johns 1997). It is estimated that only 12% of the remaining area of Asian tropical forest was in large blocks of forest (more than 400 000 ha) in 1990, compared with 20% of African forests and 41% of Latin American forests (McCloskey 1993). Clearly, the amount of forest in isolated fragments is very substantial.

Calculating the global increase in the amount of forest in small fragments is difficult, as data are not often available at suitable scales, with only a few exceptions, for example, Skole & Tucker's (1993) study of Amazonian fragmentation. Correlations between deforestation and fragmentation are highly nonlinear, as deforestation in a very large expanse of forest may not create large numbers of fragments, whereas once a region is fragmented any further deforestation is likely to create more and/or smaller fragments. Synergistic interactions between fragmentation and drought and fire further complicate comparisons (Laurance 2004). Broadly, Southeast Asia, West Africa, Central America, southern and eastern Amazonia, and Brazil's Atlantic coast contain extensive areas of highly fragmented forest. In comparison, central Congo and central and western Amazonia are relatively unfragmented. Achard *et al.* (2002) provide what is to our knowledge the first global estimate of rates of change in tropical forest fragmentation. Using satellite data to calculate the amount

of forest in a mapping unit that contains 40–70% natural forest cover, they estimate that a total of 37.8 million ha of forest was fragmented by 1990, rising to 41.9 million ha by 1997, an annual increase of 0.6 million ha yr⁻¹ (table 1, figure 2).

(j) *Lianas*

Increases in the number and biomass of large lianas over the late twentieth century in tropical forests have recently been documented in undisturbed forest plots across western Amazonia (Phillips *et al.* 2002b). The rate of increase was 1.7–4.6% yr⁻¹ over the past two decades (Phillips *et al.* 2002b). There was an average of 7.7 lianas ha⁻¹ (10 cm or more in diameter) in 1981 increasing to 12.8 ha⁻¹ in 2001. Using linear regression on averages from 5-year census intervals from 1981 to 2001 gives an annual increase of 0.28 lianas ha⁻¹ yr⁻¹ (figure 2; table 1).

4. HOW MIGHT TROPICAL FORESTS CHANGE?

We identified 10 possible drivers of change that may be causing shifts in tropical forest structure and dynamics. However, some drivers affect multiple processes, giving a total of 16 distinct hypotheses. Thus, increasing temperatures may affect either photosynthetic rates or respiration costs, or change soil temperatures altering nutrient availability; solar radiation changes, whether increases or changes in diffuse/direct proportions, may both increase growth, but via different mechanisms; increasing CO₂ concentrations may affect both light-use efficiency and water-use efficiency; nutrient deposition may increase N inputs alone and/or inputs of other nutrients; and land-use change creates forest edges, and alters the population dynamics of pioneer trees, both of which may alter forest dynamics. In the following we review the theory, results from laboratory and field experiments, and field observations pertaining to each of these hypotheses, to try to identify if the changes in drivers of the magnitude we have documented are likely to affect tropical forest structure and dynamics.

The reader should recognize that this section of the paper is by necessity somewhat limited and in part quite speculative for five reasons. First, we highlight broad hypotheses relevant to generating predictions from long-term forest plot data rather than listing all the specific mechanisms that may be affected. For example, take the effects of increasing air temperatures on growth: at the level of complexity of direct interest to ecologists, temperatures may affect potential growth rates by affecting instantaneous rates of photosynthesis. But at a deeper level, long-term temperature changes may alter the levels of various components of the photosynthetic machinery such as maximum electron transport capacity. Second, we evaluate relevant secondary effects of changes in drivers (e.g. the effects of increasing CO₂ concentrations on respiration) only if they are well documented and are expected to largely affect growth, mortality or recruitment outcomes. Third, while this review is specifically about the responses of tropical trees in mature forests, long-term experimental manipulations of intact tropical forests are largely lacking. Many of the experimental data cited are from studies of seedlings, not adult trees, many of them grown in pots and not in intact forests, often using non-

tropical species. Therefore, cautious interpretation is required, as

- (i) nonlinear scaling from the leaf to the whole plant, and to the forest stand, is likely to be the norm;
- (ii) responses to a step-change in conditions, such as increasing CO₂ concentrations to double pre-industrial concentrations, may be different from responses to chronic changes in conditions; and
- (iii) responses of plants to short-term experiments may be quite different from long-term outcomes.

Fourth, we expect different tree species will respond differently to changes in the various drivers, but reviewing the responses of different functional types to each driver is beyond the scope of this paper. Fifth, we treat each hypothesis separately but recognize that drivers of change will act on tropical forests both simultaneously and interactively. Given the almost limitless possible interactions between drivers and forest processes, our discussion of interactions and feedback loops cannot attempt to be exhaustive. Below we review the evidence that a driver may cause changes in the structure and dynamics of tropical forests. We focus a disproportionate amount of space on two strong global trends whose impacts are most actively debated: increasing atmospheric CO₂ concentrations and air temperatures.

(a) *Temperature*

Air temperatures in the tropical forest biome have increased on average by 0.26 °C per decade (Malhi & Wright 2004). Warmer temperatures increase the rates of virtually all chemical and biological processes in plants and soils, until temperatures reach the point where enzymes are denatured. The relationships are very similar for most processes, an approximately sigmoidal cubic function: zero at a minimum temperature, a nonlinear increase, with a point of inflection and peak rate falling rapidly to zero at a maximum temperature (Cannell & Thornley 1998). For each process we need to determine where on these reaction curves recent temperature changes lie. Unless most tropical forest trees are at their absolute maximum we can expect increased process rates. For any processes at their maximum temperature, large negative effects on processes are expected. A rise in temperature may affect four major processes that may in turn alter tropical forest dynamics: photosynthesis, respiration, soil nutrient availability and ontogenetic development (Saxe *et al.* 2001). We briefly review each in turn.

(i) *Temperature effects on photosynthesis*

Four component processes of photosynthesis are considered temperature dependent and relevant to plants growing in a tropical environment:

- (i) concentrations of chlorophyll and carotenoids may increase as temperature increases, which may increase C gains;
- (ii) light-saturated photosynthesis may increase as maximum rates of electron transport may increase with rising temperature, increasing C gains;
- (iii) apparent quantum yield may increase with increasing temperature, increasing C gains; and

- (iv) photorespiration is increased by higher temperatures, decreasing photosynthesis and C gains (Saxe *et al.* 2001).

The net effect of changes in these four processes in tropical forest trees in response to recent temperature increases of 0.26 °C per decade is clearly difficult to predict: are increases in photorespiration high enough to 'cancel out' extra C gains from the other three processes (if they occur)?

Are present-day midday temperatures in tropical forests high enough to cause declines in photosynthesis? Points of inflection typically occur at 35–45 °C for many high-temperature-adapted plants (Berry & Björkman 1980). Temperatures of leaves at the top of the canopy may be at the bottom of this range around midday at some locations on some days, and post-midday declines in photosynthesis have been documented (Ishida *et al.* 1999). However, separating the effects of high temperatures and daytime stomatal closure, owing to inadequate water supply, on photosynthetic rates is difficult. An experiment artificially heating leaves in the early morning and cooling leaves at midday showed that both temperature and stomatal closure depressed photosynthetic rates at midday of an *in situ* pioneer tree (Ishida *et al.* 1999). In another experiment seedlings of four dipterocarp species were exposed to increasing temperatures. Large decreases in photosynthesis occurred at different temperatures for different species, as high as *ca.* 45 °C in the species that naturally grow in large gaps and on forest edges (Kitao *et al.* 2000). Thus, there is some evidence that if maximum daily temperatures increase this may decrease photosynthetic rates and hence plant growth in some species.

Temperature increases are not occurring in isolation: simultaneous increases in CO₂ concentrations are also occurring (see § 4e). The optimum temperature for photosynthesis increases substantially with rising levels of atmospheric CO₂, as does the maximum temperature at which leaves continue to photosynthesize, and as does the photosynthetic rate at a given temperature. In addition, CO₂:O₂ ratios decrease, decreasing photorespiration (Long 1991; Norby *et al.* 1999; Morison & Lawlor 1999; Saxe *et al.* 2001; Medlyn *et al.* 2002). These general results have been demonstrated in subtropical seedlings (Sheu & Lin 1999), and have been simulated for tropical forests using an ecosystem gas-exchange model (Lloyd *et al.* 1995; Grace *et al.* 1996).

Accordingly, recent temperature increases may not lead to large decreases in photosynthetic rates. However, higher temperatures may increase vapour pressure deficits, causing stomata to close and decreasing photosynthesis. Again, the simultaneous increase in CO₂ concentrations may increase water-use efficiency, which would reduce this temperature effect, but as a result leaf temperatures may increase as stomata close, which may further affect photosynthesis.

Overall it is uncertain whether rising temperatures have increased or decreased instantaneous photosynthetic rates. However, as rising air temperatures are occurring simultaneously with increasing CO₂ concentrations and higher CO₂ decreases photorespiration and raises the optimal temperature for photosynthesis, this suggests that instan-

taneous photosynthetic rates may have increased over recent decades.

(ii) Temperature effects on respiration

Short-term experiments have shown exponential increases in respiration with rising temperature (Ryan 1991; Amthor 2000). The short-term effects of temperature on respiration appear to be kinetic effects on processes using respiratory products or the availability of labile C (Dewar *et al.* 1999; Amthor 2000). However, short-term experimental responses may overestimate increases in respiration with rising temperatures, as longer-term responses may be mediated through the effects of temperature on growth and maintenance processes, notably the supply of substrate from photosynthesis (Dewar *et al.* 1999; Amthor 2000).

Again, appropriate experiments on tropical trees are, to our knowledge, unavailable. Thus, it is unclear whether the 0.26 °C per decade increase in air temperatures may be causing increases in respiration similar to short-term experiments—a 'tax' exponentially increasing with temperature—or that respiration may be increasing more modestly as temperatures have risen, or perhaps respiration rates have altered in line with longer-term changes in photosynthetic rates? This question is currently open to debate (Clark 2004). Finally, some evidence suggests that higher CO₂ concentrations may reduce respiration, although there is much uncertainty over this (Morison & Lawlor 1999; Chambers & Silver 2004).

(iii) Temperature effects on soil nutrient availability

Rising temperatures may increase soil nutrient availability as higher temperatures increase soil organic C decomposition rates that may in turn enhance soil nutrient mineralization rates, leading to greater nutrient availability, especially for N (Silver 1998; Saxe *et al.* 2001). N mineralization rates increased following experimental soil warming of a mid-latitude hardwood forest (Melillo *et al.* 2002). However, N may not be limiting to mature trees in most tropical forests, with the probable exceptions of montane forests and those on very young or white-sand soils (Vitousek & Farrington 1997; Tanner *et al.* 1998; Sollins 1998; Martinelli *et al.* 1999; Hall & Matson 1999). Thus, increasing N availability may not cause increased growth in most tropical forests. Indeed, extra inputs may lead to soil acidification, the depletion of base cations, and the mobilizing of aluminium ions, the net effects of which may be a decrease in soil nutrient availability and plant growth rates (Matson *et al.* 1999, 2002; Martinelli *et al.* 1999; Asner *et al.* 2001). But the hypothesis that most tropical forests are P limited and not N limited is not based on experimental fertilizer additions to mature lowland tropical forests, and thus is open to debate. Seedlings grown in pots of forest soil have often not shown P limitation (Sundralingham 1983; Denslow *et al.* 1987; Burslem 1996). Likewise, seedlings grown in intact forest, either in fertilizer or trenching experiments, have not shown P limitation (Denslow *et al.* 1990; Turner *et al.* 1993; Lewis & Tanner 2000). Thus, P limitation may or may not be the norm for lowland tropical forest stands.

Rising temperatures may also increase available P, Mg, Ca or K, and where that element is limiting, forest growth may increase. Evidence in favour of this scenario is the

general trend for leaf nutrient concentrations (N, P, Ca, Mg, K) and the cycling of nutrients in leaf litter to both decrease with altitude (and hence decreasing temperatures) when sampled on the same tropical mountain (Tanner *et al.* 1998; Silver 1998). This may result from the greater immobilization of nutrients in the soil caused by slower soil organic-matter decomposition, which may be temperature controlled (Tanner *et al.* 1998; Silver 1998). Thus, higher temperatures may generally increase soil nutrient availability, and hence growth, via increases in soil organic matter decomposition rates. Again, however, appropriate experiments are lacking.

(iv) *Temperature and ontogenetic development*

Higher temperatures increase the rate of ontogenetic development in a variety of species (Morison & Lawlor 1999). If the same applies to tropical trees (although data are absent), this would increase stand-level growth and stem turnover rates, as trees would reach maturity and senesce earlier.

Is there evidence from forest stands on the impacts of temperature increases on growth? A recent paper shows a negative correlation between annual stem growth rates of a cohort of six species and mean annual daily minimum temperatures, but not mean annual daily maximum temperatures, from 1984 to 2000 (Clark *et al.* 2003). The correlation with minimum and not maximum temperatures suggests that the correlation is caused by increased respiration costs rather than decreased photosynthesis resulting from high midday temperatures.

However, as Clark *et al.* (2003) track a single cohort of trees including only those that survive the whole monitoring period and not a dynamic population of trees, this result ought to be treated with caution. Ageing populations are to be expected to exhibit a long-term decline in net stem growth as increasing numbers of trees would reach the canopy and switch (at least some) allocation from stem growth to reproduction, and/or others would reduce growth as they senesce. Furthermore, dying trees are known to exhibit slower growth before they die, and recruited trees often show vigorous growth, also contributing to a decrease in net stem growth of a cohort over time (Manokaran & Swaine 1994). The effect may be large, as only *ca.* 25% of the originally marked trees were included in the Clark *et al.* (2003) analysis. In addition, the temperature data used are from two different sites (the first spans 1984–1991, the second 1992–2000). Any mismatch of these two datasets would affect the temperature–growth correlation, especially as it is driven by three points: 1985 and 1986 with very low temperatures, from the first dataset, and 1998 with very high temperatures, from the second. However, if the temperature–growth correlations are maintained after controlling for these artefacts, then this would be good evidence to indicate that temperature changes can increase respiration costs in some tropical forest species.

Perhaps the only evidence where an entire tropical forest has been monitored as it experiences higher temperatures for a length of time is during an ENSO event. While we note that many other factors, notably decreased rainfall and increased solar radiation (from decreased cloud cover), often co-occur, comparing the growth of forests in

ENSO years with non-ENSO years may prove insightful. Three studies report stand-wide tree growth estimates for an ENSO and a non-ENSO period from forest plot data: all compare the 1997–1998 ENSO, considered the strongest of the twentieth century, and a reference period immediately preceding (Nakagawa *et al.* 2000; Condit 2001; Aiba & Kityama 2002). Mean pan-tropical forest temperatures were 0.3 °C higher in the period 1997–1998, during which a major ENSO event occurred, compared with the 1995–1996 period, and monthly average temperatures peaked at 0.9 °C higher in early 1998 (Malhi & Wright 2004).

A lowland forest plot in northwest Borneo showed a small decrease in stand-level growth during the ENSO period (forest-wide significance was not tested), as did montane forest plots in northeast Borneo (significant, attributed to drought), while several lowland forest plots in northeast Borneo showed no change in growth, and lowland forest plots in Central America showed an increase in growth (significance or magnitude not given; attributed to higher solar radiation). The results are difficult to compare as different measures of growth were used in each study. However, as increases, decreases and no change in stand-level growth have all been shown, we conclude that many tropical forest trees tolerated the warmest year of the last century without catastrophic declines in growth (but see § 4d for details on the effects of ENSO events on mortality).

Overall, the net effect of the 0.26 °C increase in air temperature on photosynthetic rates, respiration and soil nutrient availability described above is unclear. Increases or decreases in photosynthetic C gains are possible; however, increases in respiration costs may decrease growth, while nutrient availability may increase, increasing growth.

(b) *Precipitation*

Long-term changes in precipitation could alter growth rates if water becomes a limiting resource for a greater or lesser part of the year. The main region to witness a significant trend in the availability of water is the northern tropical forest belt in Africa (Malhi & Wright 2004). If water availability is decreased, as may have occurred across much of tropical Africa over the past two decades, and became more limiting, then this could decrease growth rates. Drought is well known to decrease growth, and has been clearly experimentally demonstrated in mature old-growth tropical forest (Nepstad *et al.* 2002). However, given the lack of any consistent global rainfall trends, changing rainfall is unlikely to be a major cause of any globally observed changes in forest dynamics.

(c) *Solar radiation*

If satellite data showing an increase in incoming solar radiation are correct, then increases in forest growth are predicted, as shown in experiments (Graham *et al.* 2003). However, theory predicts two opposite outcomes for tropical forests in response to global dimming, if it is occurring (Stanhill & Cohen 2001). Firstly, a long-term reduction in solar radiation would decrease photosynthesis, and hence growth and stand biomass, if trees are light limited. Alternatively, the reduction in total solar radiation is likely to be accompanied by an *increase* in diffuse solar radiation (Stanhill & Cohen 2001). Theoretically, this is expected to

increase total canopy photosynthesis, as diffuse light can penetrate deeper into a canopy by reducing the self-shading of leaves in the canopy (Roderick *et al.* 2001). This effect—that plant canopies can use diffuse radiation more efficiently than direct radiation—has been demonstrated in a North American hardwood forest using measurements before and after the 1991 Mt Pinatubo volcanic eruption, which in 1992 decreased global direct solar irradiance by *ca.* 3% but increased diffuse irradiance by *ca.* 9% (Gu *et al.* 2003). Midday photosynthesis of the forest rose by 23% under cloudy conditions in 1992 compared with a control year. Thus, increasing the diffuse fraction of incoming solar radiation may cause large increases in forest growth.

(d) *Climatic extremes/El Niño–Southern Oscillation*

ENSO events can cause increased tree mortality, both from intense drought in the El Niño phase and intense rainfall in the La Niña phase, as has been well demonstrated by forest inventories that span both an ENSO event and a reference period before the ENSO event. Examples of increasing mortality include the response of Central American forests to the 1982–1983 (Lieberman *et al.* 1990; Condit *et al.* 1995) and the 1997–1998 (Condit 2001) El Niño events. Central Amazonian and Southeast Asian forests also exhibited higher tree mortality during the 1997–1998 event (Nakagawa *et al.* 2000; Williamson *et al.* 2000; Aiba & Kityama 2002; Potts 2003). However, not all forests have responded with increased mortality to ENSO events (Phillips 1995; Aiba & Kityama 2002).

ENSO events may also cause changes in plant growth owing to intense drought, generally higher air temperatures and higher solar radiation levels caused by reduced cloudiness associated with the drought. Three of the studies mentioned in the previous paragraph also monitored the growth of tropical forest stands over the 1997–1998 ENSO event and the years immediately preceding. The results were inconsistent, showing growth decreasing, increasing or remaining unchanged when comparing the two periods (Nakagawa *et al.* 2000; Condit 2001; Aiba & Kityama 2002). The net effect of strong ENSO events appears to be a general increase in tree mortality, but effects on growth have been inconsistent. However, it has been experimentally demonstrated that reducing rainfall by 50% in an eastern Amazonian forest causes a reduction in above-ground net primary productivity by *ca.* 25% (Nepstad *et al.* 2002). Increases in mortality are also expected from increases in other extreme climatic events, for example windstorms (Nelson *et al.* 1994).

The impact of ENSO events on tree mortality can be severe, but mortality may increase for only a very short period of time, rapidly returning to pre-ENSO levels (Williamson *et al.* 2000). Across Amazonia this short-term increase in mortality has not caused large declines in above-ground biomass. Out of 59 long-term forest monitoring plots from across the Amazon basin used in a study of biomass change, 45 included the 1997–1998 ENSO event, and out of these 37 (82%) had increased in biomass by the time they were last re-measured between 1999 and 2002 (Baker *et al.* 2004). This compares with 12 out of 14 plots (86%) that increased in biomass over a monitoring period that did not include an ENSO event. Overall,

these forest plots across Amazonia increased in above-ground biomass despite the monitoring period spanning the strongest ENSO event of the twentieth century.

The evidence to date suggests that ENSO droughts, which may be very important for some species, have increased mortality rates, but that for many forest stands the biomass of the dead trees that is lost, as mortality is temporarily increased, is rapidly accumulated by the surviving and newly recruited trees. At present these droughts do not appear to be causing major longer-term changes in forest structure. This may be because ENSO events are occasional short-lived events that have occurred quasi-regularly for centuries (Tudhope *et al.* 2001).

(e) *Carbon dioxide*

Atmospheric CO₂ concentrations are increasing by 1.5 p.p.m. yr⁻¹. CO₂ is a key substrate of photosynthesis. The general response of plants to this increase may be an increase in resource-use efficiency, especially higher rates of photosynthesis, which improves light-use efficiency, and decreasing stomatal conductance and transpiration, which improves water-use efficiency. In addition, any acclimation of photosynthesis to higher CO₂ concentrations would reduce key enzyme usage, notably Rubisco, increasing whole-plant nutrient-use efficiency (Drake *et al.* 1997; Saxe *et al.* 1998). We discuss the potential effects of rising CO₂ concentrations on light-use efficiency, water-use efficiency and nutrient-use efficiency in turn.

(i) *Carbon dioxide effects on light-use efficiency*

Short-term increases in photosynthetic C gains and plant growth in response to increases in CO₂ concentrations have been shown experimentally for many species. This is expected because CO₂ is a substrate for Rubisco, and higher CO₂ levels increase CO₂:O₂ ratios, which reduces photorespiration (Saxe *et al.* 1998; Curtis & Wang 1998). While most of these experiments have occurred in pots, and often using temperate species, increased growth has been demonstrated *in situ* for tropical tree seedlings (Würth *et al.* 1998a). A meta-analysis of many experiments also shows that growth under high CO₂ concentrations increases both the total plant leaf area and unit leaf rate of plants. The relative effects, including growth-rate increases, are higher under lower light conditions, i.e. light-use efficiency increases (Curtis & Wang 1998). This effect has also been experimentally demonstrated for an *in situ* forest stand of loblolly pine exposed to higher CO₂ concentrations, which increased their light-use efficiency by 27% (DeLucia *et al.* 2002).

While the effects of increasing CO₂ concentrations on relatively well-fertilized and watered plants grown in pots are undisputed, several important questions remain when considering whether trees growing in undisturbed tropical forests have responded to the recent increases in CO₂ concentrations. We briefly address each question in turn.

- (i) Are tropical trees C limited?
- (ii) Are potentially competing tropical forest trees growing together in stands expected to respond to increased CO₂?
- (iii) Are tropical forests growing on poor-fertility soil expected to respond to increasing CO₂ concentrations?

- (iv) Will demonstrated short-term responses persist over the longer term, or will photosynthetic acclimation (downregulation) occur?
- (v) Will either mature or maturing trees respond, and if both groups respond, which would respond most?

(i) Are tropical trees C limited? There is no direct evidence that tropical trees are CO₂ limited, as there are no experiments increasing CO₂ for stands of tropical trees. However, elevated growth with increases in CO₂ of *in situ* tropical tree seedlings suggests that extra CO₂ may result in extra growth, at least for some seedlings (Würth *et al.* 1998a). In addition, experiments exposing complete stands of temperate pine and deciduous trees to elevated CO₂ concentrations both show substantial increases in net primary productivity by 26% and 21%, respectively, suggesting that tropical forests may exhibit a similar response (Norby *et al.* 2002; Hamilton *et al.* 2002).

By contrast, one indirect line of evidence suggests that mature tropical trees are not C limited and will show little, if any, response to increasing CO₂ concentrations. If a leaf or branch of a mature tree is exposed to high CO₂ concentrations, the leaves increase instantaneous photosynthetic rates and increase their levels of NSCs in leaf and/or woody tissues (Würth *et al.* 1998b; Lovelock *et al.* 1999). This has been interpreted to indicate that the tree cannot use the extra C being assimilated, and therefore that it is not C limited (Körner 2003). In addition, the consistently high levels of NSCs in mature trees from both temperate and tropical regions are given as further evidence of a lack of C limitation in mature trees (Körner 2003). The argument runs that if C were in short supply for growth, NSC concentrations should not be so high in leaves and branches.

However, other interpretations of initially high NSC levels and their increase following exposure to higher CO₂ are possible. NSCs in leaves and woody tissues may have—as yet unidentified—functions, so what appear to be ‘high’ levels may actually be optimal. Levels of NSCs are very hard to deplete: even a major fruiting event—a severe drain on resources—does not change levels. But extreme exogenous changes, such as major defoliation, can cause trees to reduce their NSCs levels, as presumably these NSCs are used to produce new leaves (Körner 2003). Perhaps, then, NSCs are a plant’s ‘insurance policy’ against severe structural damage, and investment in this is a better strategy for increasing overall fecundity than higher investment in immediate growth with no ‘insurance policy’.

Similarly, the increase in NSCs on exposure of individual branches or leaves to high CO₂ levels may have alternative explanations. If NSC levels represent an optimum allocation between assimilate for growth and assimilate for NSCs (whatever their function) under a limited C supply, then if higher CO₂ levels cause the production of extra assimilate, as shown in experiments, then allocation to growth and allocation to NSCs would be expected. Thus, the documented rise in NSCs may reflect this (Würth *et al.* 1998a; Lovelock *et al.* 1999). This was seen in an experiment growing *in situ* tree seedlings under high CO₂, where both total plant biomass and NSCs increased significantly (Würth *et al.* 1998b). Furthermore, for a light-limited mature tropical tree, growth, reproduction (as

flowers) and leaf NSCs all increased with experimental lighting over a year (Graham *et al.* 2003). That NSC levels increased when a tree was exposed to more light—which is known to be limiting—is good evidence to suggest that just because a plant increases NSC levels in response to high atmospheric CO₂ concentrations does not necessarily indicate that it is not limited by C. Indeed, the reverse may be true. Overall, the indirect evidence that tropical trees are C limited appears weak, but until experiments elevating CO₂ levels across old-growth stands of tropical trees are conducted this issue is likely to be open to debate.

(ii) Are potentially competing tropical forest trees growing together in stands expected to respond to increased CO₂? Experiments where tropical seedlings of several species were grown together in competition under contemporary and higher CO₂ concentrations have shown no net increase (Lovelock *et al.* 1998), and small non-significant increases in growth for all species combined (Reekie & Bazzaz 1989; Körner & Arnone 1992; Arnone & Körner 1995; Rosenthal 1998). However, these experiments have all been of low replication and short duration, and follow the standard practice of using ambient (highest for 20 million years) and higher CO₂ concentrations.

The two experiments exposing whole forest stands to higher CO₂ concentrations both show that trees growing in stands did increase their growth rates markedly compared with controls (Hamilton *et al.* 2002; Norby *et al.* 2002). In the loblolly pine study the understory hardwood trees (which compete with the overstorey pines) increased their growth by one-third more than did the pines, in response to higher CO₂ (Hamilton *et al.* 2002). Overall, the evidence suggests that competition is likely to alter and complicate the response of individual plants to CO₂, but not to remove it.

(iii) Are tropical forests growing on poor-fertility soil expected to respond to increasing CO₂ concentrations? Plants grown under low-nutrient conditions show responses to elevated CO₂, but show consistently lower absolute increases than well-fertilized plants do (Curtis & Wang 1998). This has been shown in an open-top chamber experiment using tropical seedlings (Winter *et al.* 2001). Whether plants grown under low-nutrient conditions consistently show lower proportional responses to elevated CO₂ is the subject of debate (Lloyd & Farquhar 1996, 2000; Poorter 1998; Norby *et al.* 1999). First, any increase in C substrate without a commensurate increase in limiting soil nutrients would reduce growth in comparison to that possible with a commensurate increase in limiting soil nutrients. This effect is proportionately greater in low-nutrient situations, and favours greater responses to elevated CO₂ by well-fertilized plants. Second, poorly fertilized plants may have higher relative respiration costs compared with well-fertilized plants (Lloyd & Farquhar 1996, 2000). Increasing photosynthetic rates by elevating CO₂ levels increases the amount of C available for growth relative to respiration, so this process favours the greatest increases by poorly fertilized plants. Together, the two processes suggest that positive growth responses to elevated CO₂ are possible under both low- and high-nutrient conditions, and that these may be proportionately similar increases (Lloyd & Farquhar 1996).

Analyses of changes in forest growth from permanent sample plots across South America may provide the first data from tropical forests relevant to this debate. Fifty permanent sample plots were split into a group of faster-growing forests (predominantly on higher-fertility soils) and a group of slower-growing forests (predominantly on lower-fertility soils), based on their stand-level growth rate. Over time the fast-growing group of forests had significantly greater absolute increases in stand-level growth than did the slow-growing forests. However, the *proportional* increases in stand-level growth were similar in both forest groups (Lewis *et al.* 2004). These results—higher absolute changes and similar relative changes in growth—are consistent with changes predicted by Lloyd & Farquhar (1996, 2000) for plants growing on more- and less-fertile soils in response to increasing CO₂ concentrations (or any other limiting resource which may have increased forest growth rates). Both theory and the limited available data suggest that forests growing on poor soils will respond to increasing CO₂ concentrations, albeit less so, in absolute terms, than forests growing on more nutrient-rich soils.

(iv) Will demonstrated short-term responses persist over the longer term, or will photosynthetic acclimation (downregulation) occur? Downregulation is the inability of the plant to use the extra C source at its new higher rate owing to either environmental limitations (nutrients, water) or inherent metabolic limitations. A meta-analysis of elevated CO₂ experiments by Curtis & Wang (1998) did not document downregulation, but most of these experiments were short term. The two experiments exposing whole forest stands to elevated CO₂ have not shown large decreases in net primary productivity over 3–4 years of monitoring (Hamilton *et al.* 2002; Norby *et al.* 2002). There are no long-term tropical studies on responses to CO₂ to call upon.

A recent synthesis of four long-term studies where non-tropical trees have been grown for up to 30 years in elevated CO₂ (three open-top outdoor chambers, one natural CO₂ vent) showed considerable increases in above-ground biomass in the short term, which, on average, decreased exponentially over time but still showed *ca.* 20% higher growth after 30 years' exposure to elevated CO₂ (Idso 1999; Idso & Kimball 2001). Extrapolating this trend predicts that a net increase in biomass over a century of *ca.* 10% under high CO₂ compared with controls. This suggests substantial, but not complete, downregulation over the longer term.

(v) Will either mature or maturing trees respond to increasing CO₂, and if both respond, which will respond most? Mature trees allocate some resources to reproduction while juveniles do not. Thus, mature individuals may be expected to show smaller proportional increases in growth rates compared with juvenile trees as CO₂ levels increase, as some of the increased availability of assimilate is very likely to be diverted to increasing reproductive effort. Thus, juvenile trees may respond—in terms of growth—much more than mature trees.

Mature individuals of five species growing naturally near a CO₂ spring did not show significant increases in growth compared with controls (Tognetti *et al.* 2000), but juvenile trees did (Hattenschwiler *et al.* 1997) and reached adult stature earlier (Tognetti *et al.* 2000). However, these

results may be influenced by juvenile plants' receiving higher CO₂ concentrations than mature plants. This is because the gas from the CO₂ springs becomes more mixed with air with ambient CO₂ concentrations with height from the ground. Hence, as the trees get taller (more mature) they may be exposed to progressively lower CO₂ concentrations. Meanwhile, 4 years of directly increased CO₂ concentrations over temperate loblolly pine stands caused trees to mature earlier and at a smaller size, and to produce more seed than controls (LaDeau & Clark 2001). The general response of juvenile trees to higher CO₂ may be an acceleration of maturity perhaps followed by an intensification of reproductive effort.

Any increase in photosynthetic light-use efficiency for plants that are near their light-compensation point will result in large proportional increases in photosynthesis and therefore growth. Thus, severely light-limited trees, including the juveniles of the canopy tree species, are likely to be very responsive to an increase in CO₂ concentrations (Würth *et al.* 1998a). This may have occurred in a large forest plot in Central America, where increases in biomass over 20 years of monitoring were modest for larger trees, but the smallest trees (1 cm diameter) showed large increases in biomass (Chave *et al.* 2003). One likely response to an increase in light-use efficiency is an increase in stem density, above a minimum threshold of measurement, as trees tolerate progressively lower light conditions. Consistent with this, the density of trees that are 10 cm or more in diameter has increased across a network of long-term forest plots in South America (Lewis *et al.* 2004).

Overall, the limited evidence suggests that while both juvenile and mature individuals are predicted to respond to rising CO₂ concentrations, it appears that juvenile trees may show proportionately greater responses to increasing CO₂ concentrations than mature trees.

(ii) Carbon dioxide effects on water-use efficiency

Tropical trees, like other plants, are expected to decrease stomatal conductance in response to increasing CO₂ concentrations, which will increase water-use efficiency. However, recent evidence from more realistic experiments in natural communities, including mature tropical trees, is more ambiguous than earlier work (Körner & Würth 1996; Curtis & Wang 1998; Saxe *et al.* 1998; Körner 2000). If water-use efficiency increases, this would mean an increase in C gains per unit of water, and, all other things being equal, an increase in growth when water is a limiting resource. In addition, less allocation to roots would be expected. Whether reduced stomatal conductance translates into reduced evapotranspiration and increased soil moisture depends in part on the canopy (including if the leaf-area index increases with increasing CO₂) and possible planetary boundary-layer feedbacks resulting from lower humidity and higher temperatures. Furthermore, decreased transpiration may further increase leaf temperatures, which may decrease photosynthetic C gains. Some increase in water-use efficiency is expected, but some extra C gains when water would have been limiting may be offset by higher leaf temperatures and reductions in atmospheric humidity.

Structural changes may also occur in response to improved water-use efficiency caused by CO₂. Current

evidence suggests that an important factor limiting tree height is hydraulic stress and the danger of cavitation (Midgley 2003). Improved water-use efficiency will reduce tension in the water column that trees experience for any given canopy height, so it may be reasonable to expect that tropical trees, especially in seasonally dry environments, may respond to elevated CO₂ with an increase in average and maximum height. This may be accompanied by a changed—more elongated—diameter/height/biomass allometric relationship. Again, experimental tests of this hypothesis are currently unavailable.

(iii) *Carbon dioxide effects on nutrient-use efficiency*

Theoretically, any acclimation of photosynthesis during long-term exposure to higher CO₂ concentrations would reduce key enzyme usage, and thus each leaf would require fewer nutrients, leading to an increase in nutrient-use efficiency (Drake *et al.* 1997). This would increase the resources a tree has available to invest in acquiring the resource it is most limited by. A shift in root : shoot ratios is expected, with more resources going below ground in nutrient-limited plants, or more resources above ground for light-limited plants. Experimental results on root : shoot ratio shifts are inconclusive, but these experiments are all short term (Curtis & Wang 1998; Norby *et al.* 1999).

(f) *Nutrient depositions*

If nutrient depositions have increased, the responses of tropical forests will depend upon which nutrient has increased and whether the trees in a given forest are limited by that nutrient. We discuss above whether lowland tropical forests are N limited, P limited or limited by some other nutrient (see § 4a). In summary, if N is limiting and N deposition increases, then growth may increase. However, if N is not limiting, extra N inputs may lead to soil acidification, the depletion of base cations and the mobilizing of aluminium ions, the net effects of which may be a decrease in soil-nutrient availability and plant growth rates (Matson *et al.* 1999, 2002; Martinelli *et al.* 1999; Asner *et al.* 2001). If P is limiting and P deposition increases (Artaxo *et al.* 2002), then growth may increase. Likewise if other micro-nutrients increase and they are limiting, growth may increase. Overall, until it is known which nutrient or nutrients are limiting forest growth, robust predictions of changes in forest growth with additional nutrient inputs are very difficult.

(g) *Ozonelacidic depositions*

Forests near areas of industrialization and biomass burning may experience high tropospheric O₃, SO₂ and other acidic depositions. Plants grown under high O₃ levels exhibit decreased growth and visible damage (Reich & Amundson 1985; Skärby *et al.* 1998; Chappelka & Samuelson 1998; Innes & Haron 2000). O₃ enters the stomata where it oxidizes one of several chemical compounds, which then reduces cell membrane integrity affecting their ability to transport chemical substances and maintain homeostasis. Reduced photosynthetic rates can occur either via stomatal closure and/or a loss of Rubisco activity (Skärby *et al.* 1998, and references therein).

SO₂—alongside various N compounds—is a major source of acidic depositions. Plants grown under high SO₂

exhibit decreases in growth and visible damage (Winner *et al.* 1985). SO₂ enters the stomata, where it can directly affect the ability of mesophyll cells to fix CO₂, oxidize cell membranes, alter enzymes with disulphide bonds and oxidize chlorophyll, among other effects (Winner *et al.* 1985, and references therein). Decreased photosynthetic rates and growth are expected (Keller 1985).

Various pollutants in combination, including O₃ and SO₂, are thought to have caused major forest die-back in European and North American temperate forests near areas of industrial activity (Skärby *et al.* 1998; Chappelka & Samuelson 1998). Such effects have recently been documented in trees in Brazil's Atlantic rainforest, near areas of industrialization (Moraes *et al.* 2003) and in areas of the subtropics that have undergone rapid industrialization (Innes & Haron 2000).

(h) *Hunting*

The preferred prey of hunters are overwhelmingly herbivores, which disperse seeds and eat seeds and seedlings (Robinson & Bennett 2000; Wright *et al.* 2000). Their removal may therefore affect the regeneration of some species and affect plant regeneration more generally by favouring the competitive release of some groups of species. Specifically, in terms of altering tropical forest dynamics, the hunting of frugivores may reduce the dispersal of large-seeded animal-dispersed species, benefiting smaller-seeded animal- and wind-dispersed trees, which on average have higher growth and turnover rates (Phillips 1996; Wright *et al.* 2000). Several studies have shown that hunting reduces frugivore density, which in turn alters seedling regeneration (Dirzo & Miranda 1990; Asquith *et al.* 1997; Wright *et al.* 2000).

(i) *Land-use change*

Forest fragmentation and isolation lead to a variety of impacts on tropical tree populations that affect forest dynamics, by

- (i) changing the microclimate that trees grow in, notably decreasing soil moisture (water availability) and increasing air temperatures owing to warmer air from non-forested areas penetrating into remaining forested areas (Kapos 1989; Kapos *et al.* 1997); and
- (ii) increasing the wind speeds that tropical trees encounter, as winds strike the new edge of the forest, increasing mortality rates, as shown in central Amazonian and Australian forest fragments (Laurance 1997; Laurance *et al.* 1998a).

Habitat fragmentation also affects tree recruitment patterns (Benitez-Malvido 1998; Laurance *et al.* 1998b; Curran *et al.* 1999), both directly (as a result of increasing tree fall disturbances, which increase light levels in the understorey) and indirectly (as a result of altered faunal communities, which can affect herbivore and seed predation). These effects may occur over large spatial scales, on the order of at least several kilometres from forest boundaries (Curran *et al.* 1999; Gascon *et al.* 2000; Laurance 2000).

In addition, habitat fragmentation may alter forest dynamics indirectly, by increasing the numbers of pioneer and gap-demanding non-pioneer trees, which, being good

dispersers, may flood the remaining forest with their seeds, increasing the proportion of pioneer recruits in the remaining forest. As pioneers have faster growth and stem turnover than non-pioneers (Manokaran & Swaine 1994; Condit *et al.* 1999), these changes would increase stem turnover and stand-level growth rates (Lewis 1998). Appropriate experiments have not been conducted; however, pioneer trees were more rapidly recruited into small forest fragments in central Amazonia compared to control plots (Laurance *et al.* 2002), while seedlings of pioneer species were recruited into experimental gaps near forest edges, but not far from edges in continuous forest, in the same Amazonian forest (Lewis 1998).

(j) *Lianas*

Lianas are structural parasites that decrease tree growth and increase mortality, and are mostly disturbance adapted (Schnitzer & Bongers 2002). Why lianas may be increasing in number and basal area is unclear, but this may be due to increasing CO₂ concentrations, as there is evidence of greater growth responses of lianas compared with trees from experiments with elevated CO₂ levels (Granados & Körner 2002). An alternative explanation is that the increase is caused by elevated stem turnover, which is increasing the frequency of disturbance and favouring an increase in disturbance-adapted taxa such as lianas (Phillips & Gentry 1994). As liana infestations rise, increases in tree mortality rates, lower stand biomass and possibly reduced tree growth rates may be expected.

5. PREDICTIONS OF CHANGES IN TROPICAL FORESTS

Different drivers of change will initially force different processes, and often have different distributions in time and space. These properties allow us to state testable predictions for each hypothesis, which, when compiled as suites of predictions, demonstrate that each driver should leave a unique fingerprint or 'signature' in permanent sample plot data. We now give unique predictions in response to each driver. This suite of testable predictions is compiled in table 2.

(a) *Temperature*

We can make two sets of predictions, one for if rising temperatures increase growth and one for if rising temperatures decrease growth (table 2). The unique prediction is that growth and biomass increases/decreases would correlate with long-term trends in temperature. If growth rates were best correlated with mean daily minimum temperatures, this would suggest that changes in respiration were dominating the pattern. If correlations were best between growth rates and mean daily maximum temperatures, then the impacts of temperature on photosynthetic rates would be the most promising candidate. If growth rates were correlated with temperature changes, but effects are disproportionately large and positive in forests growing on nutrient-poor soils, then soil warming is the most likely mechanism.

Differing regional-scale responses may provide further information. Central African forests in particular are consistently cooler than many other tropical forest regions (Malhi & Wright 2004), so if changes in growth are less

or absent in African forests compared with Southeast Asian or South American forests, this may indicate that temperature changes are important. Also, some regions (notably western Amazonia) experienced cooling in the 1950s and 1960s owing to local climatic oscillations. Few plot data are available from this period, but if these cooling trends recur, then patterns of temperature response may be reversed. Spatially and temporally consistent results like these scenarios could provide good evidence of a fingerprint of increasing temperatures (cf. Parmesan & Yohe 2003).

(b) *Precipitation*

Annual rainfall and the length and the intensity of the dry season have not altered consistently across the tropical forest biome, but drying has increased markedly across the northern Congo basin over at least the past two decades (Malhi & Wright 2004). Thus, changing precipitation cannot drive biome-wide shifts in dynamics, but may dominate patterns in some areas. The unique prediction from this hypothesis is that changes in growth will correlate with long-term changes in rainfall patterns, but only in seasonal forests and only where changes in rainfall reduce or extend the intensity of water stress in the dry season.

(c) *Solar radiation*

It is currently unclear exactly what changes in solar radiation have occurred, and whether changes in direct/diffuse components have altered over recent decades. Any changes in solar radiation patterns can be expected to have a spatial and temporal pattern—we can predict that changes in forest growth will track these changes.

(d) *Climatic extremes/El Niño–Southern Oscillation*

The unique prediction for the climatic extremes/ENSO-drought hypothesis is that mortality rate increases and stand biomass decreases will correlate with the spatial distribution of ENSO effects and/or other known extreme climatic events. For example, areas such as southwestern Amazonia, which are largely unaffected by ENSO events, would be expected to show little or no changes in forest dynamics and biomass. By contrast, in northeastern Amazonia, which is more strongly affected by ENSO events, larger increases in mortality rates and reductions in biomass would be predicted. In addition, by comparing African forests with Amazonian and Southeast Asian forests, the effects of temperature and drought may be teased apart as ENSO events cause warmer, but not drier, conditions in African forests.

(e) *Carbon dioxide*

As atmospheric CO₂ concentrations rise, and if trees increase their light-use efficiency in response, increases in net growth from forest stands are predicted, with the greatest increases in forests where other factors are least limiting (aseasonal forests growing on nutrient-rich soils). Growth increases in forests growing on nutrient-poor soils are also expected, although these forests are expected to show smaller absolute increases than forests on higher-fertility soils. Within a given forest stand, those individuals least limited by other resources may respond most; thus, the largest relative increases may be from juvenile trees,

Table 2. Predictions for 16 hypotheses that may have caused changes in tropical forest dynamics during the latter part of the twentieth century. (Abbreviations: y, yes; n, no; ?, response unclear. Multiple tests are applicable to more than one external forcing factor, e.g. chemical factor CO₂, or N deposition. Each hypothesis gives a unique 'fingerprint' of expected responses to the tests.)

	hypothesis															
	1 ^b	2	3	4	5 ^b	6	7	8	9	10 ^b	11	12	13	14	15	16
multiple tests																
growth, recruitment and biomass ↑ especially where physical factor ↑	?	n	y ^a	n	?	y ^a	n	n	n	n	n	n	n	n	n	n
growth, recruitment and biomass ↑ especially where physical factor ↓	?	y	n	n	?	n	y ^a	n	n	n	n	n	n	n	n	n
growth, recruitment and biomass ↑ especially where chemical factor ↑	n	n	n	n	n	n	n	y ^a	y ^a	?	y	n	n	n	n	n
growth, recruitment and biomass ↑ especially where chemical factor ↓	n	n	n	n	n	n	n	n	n	?	n	y ^a	n	n	n	n
recruitment rate ↑ only where biological factor ↑	n	n	n	n	n	n	n	n	n	n	n	n	y ^a	y ^a	y ^a	y ^a
mortality rate ↑ especially where physical factor ↑	y ^a	y ^a	y ^a	n	n	y ^a	y ^a	n	n	n	n	n	n	n	n	n
mortality rate ↑ especially where chemical factor ↑	n	n	n	n	n	n	n	y ^a	y ^a	?	n	y ^a	n	n	n	n
mortality rate ↑ especially where biological factor ↑	n	n	n	n	n	n	n	n	n	n	n	n	y ^a	y ^a	y ^a	y ^a
single tests																
stand biomass ↑	?	n	y [?]	n	?	y	n	y [?]	y [?]	?	y	n	n	n	n	n
stand biomass ↓	?	y	y	y	?	n	y	n	n	?	n	y	n	y	n	y
stand stem density ↑, as mortality lags recruitment	?	n [?]	y	n	?	y	n	y	y	?	y	n	n	n	n	y [?]
stand stem density ↓, as recruitment lags mortality	?	y [?]	n	y	?	n	y	n	n	?	n	y	n	y	n	y
mortality change and growth change positively correlated	?	y	y [?]	y [?]	?	y [?]	n	y [?]	y [?]	?	n	n	y	n	y	n
recruitment change and growth change positively correlated	?	y	y	y	y	y [?]	n	y	y	?	y	n	y	n	y	n
structurally similar sites respond similarly	y	y	y	y [?]	n	y [?]	n	y	y	n	n	n	n	n	n	?
recruits larger and faster growing in later censuses	y	n	y	y	n	y	n	y	y	n	n	n	y	n	y	n
changes correlate with distance from the nearest edge	n	n	n	n	n	n	n	n	n	n [?]	n [?]	n [?]	n [?]	y	y	?
removal of pioneers removes effects	n	n	n	n	n	n	n	n	n	n	n	n	n	n	y	n
changes increasingly dominated by large trees	n [?]	n [?]	n [?]	n [?]	y [?]	n [?]	?	n [?]	n [?]	n [?]	n	?	n	y ^a	n	y [?]
increase in mortality dominated by deaths of earlier recruits	n	n	n	n	n	n	n	n	n	n	n	n	y	n	y	n
large trees increasingly prone to death	n [?]	n [?]	n [?]	n [?]	?	n [?]	y [?]	n [?]	n [?]	y [?]	n	y [?]	n	y	n	y
small trees increasingly prone to death	n	n [?]	n	n	n	n	?	n	n	n	n	n [?]	y	n	y	n
mortality ↑ restricted to a few species	n	n	n	n	n	n	n [?]	n	n	y [?]	n	n [?]	y	n	y	y [?]
magnitude of change correlates with soil fertility	y ^a	n [?]	y ^a	y ^a	y ^a	y ^a	n	y ^a	y ^a ?	y ^a	y ^a	n [?]	y [?]	n	?	n
magnitude of change correlates with soil water	y ^a	n [?]	y ^a	y ^a	y ^a	y ^a	n [?]	y ^a	y ^a	n	n	n [?]	n	n	n	n
recruitment ↑ correlates with level of defaunation	n	n	n	n	n	n	n	n	n	n	n	n	y	n [?] ^b	n [?] ^b	n

^a These hypotheses can be further distinguished, as different mechanisms predict different responses, e.g. maximum growth rate increases under hypothesis 1 will be at nutrient-rich aseasonal sites that warmed, whereas under hypothesis 3 maximum growth rate increases will be at nutrient-poor aseasonal sites.

^b There is uncertainty whether changes in the driver cause increases or decreases in growth.

especially in disturbed areas (where light and nutrients may be more abundant). This may increase stem and biomass turnover, as gap durations decrease and average tree lifespans shorten, creating a positive feedback that promotes further forest disturbance and hence increased growth. Increasing light-use efficiency will decrease the light compensation point of trees, which we predict will lead to an apparent increase in stem recruitment in forest plot data. Furthermore, as more trees are at the minimum threshold for measurement (usually 10 cm diameter at breast height) in a given light environment, this would also increase stem density above the same threshold. If the above-mentioned changes occur, more rapid increases in growth, recruitment and mortality rates may be expected than the changes in stand-level biomass and stem density, which may change more modestly. This general scenario has been theoretically predicted by Norby *et al.* (1999) for temperate forests and by Körner (1998, 2003) for tropical forests.

If plants increase their water-use efficiency the unique prediction is for increases in growth in forests only where water is limiting for part of the year (i.e. no change in the growth or biomass of aseasonal forests is predicted), and increased growth would occur even when no changes in rainfall had occurred. If trees increase their light-use and water-use efficiency simultaneously in response to rising CO₂ concentrations, the greatest absolute increases in growth would be expected from forests growing on nutrient-rich soils where water is limiting for part of the year. Also, increasing water-use efficiency is predicted to cause changes in mature-tree canopy height wherever hydraulic stress is a limiting factor on tree height.

(f) *Nutrient deposition*

If increases in nutrient deposition occur, whether N or other nutrients, we can predict that forest growth and biomass will alter in forests only where the deposition of nutrients has occurred *and* that nutrient is limiting. In general, elevated nutrient deposition is expected downwind of biomass burning and near areas of industrialization and intensive agriculture. Rates of nutrient deposition are likely to have a strong spatial pattern: N deposition rates are likely to be large in Southeast Asia compared with South America and Africa owing to the much higher levels of intensive agriculture and industrialization; thus, if changes in growth show large continental-scale differences this may be evidence that nutrient deposition is causing changes in some areas. If, in general, forests are not N limited, increased soil acidification may occur, decreasing growth rates and biomass.

(g) *Ozonelacidic depositions*

If tropospheric O₃ and acidic depositions are altering forest dynamics then we can uniquely predict that declines in growth rates and increases in mortality will correlate with increases in tropospheric O₃ and acid deposition levels. These effects will be greatest near biomass-burning sites and industrial activity. Like nutrient deposition, while locally and regionally important (most likely in Southeast Asia), changes in O₃ and acid depositions are unlikely to explain biome-wide shifts in dynamics over recent decades.

(h) *Hunting*

At sites where hunting pressure has increased and the competitive release of smaller-seeded species has occurred, we predict an increase in recruitment and growth rates at these sites only. Uniquely, only changes in forests that have experienced increased hunting pressure are predicted.

(i) *Land-use change*

If habitat fragmentation, and hence edge creation, is the cause of changes in forest dynamics we predict that changes in recruitment, mortality and biomass would be correlated with distance from forest edges. However, if habitat fragmentation leads to pioneer trees flooding the remaining forest, and thus increasing growth and stem turnover rates, then these changes should be directly attributable to an increase in the density of individuals of pioneer and gap-demanding non-pioneer species within long-term forest plots.

(j) *Lianas*

If lianas are driving changes in forest dynamics or are themselves responding to changes in a driver, then uniquely, changes in dynamics should be correlated with changes in the density of large lianas and their net biomass.

6. DISCUSSION

(a) *General patterns*

We have identified 10 different possible drivers that may cause widespread changes in tropical forest dynamics: temperature, precipitation, solar radiation, climatic extremes (including ENSO events), atmospheric CO₂ concentrations, nutrient deposition, O₃/acid depositions, hunting, land-use change and increasing density of lianas (table 1; figure 2). In addition, some of the environmental drivers that we identify may alter multiple processes; for example, increasing atmospheric CO₂ concentrations may increase both light-use efficiency and water-use efficiency. In total we identify 16 plausible hypotheses (table 1). These drivers and hypotheses have varying degrees of uncertainty at each stage of our framework. They range from whether a particular driver has actually changed to theoretical predictions of the ecological responses to the change, to the evidence as to what the probable responses of forests would be to such an environmental change, to whether the magnitude of such a change is ecologically meaningful. We summarize these major areas of uncertainty for each driver in table 1, and discuss each in turn below. Finally, we assess which drivers are most consistent with published changes in the growth, recruitment and mortality of South American tropical forests from long-term forest plot data, and how the drivers may change in the future.

Spatially, the drivers have distinct patterns: some have relatively uniform changes at the pan-tropical scale (CO₂, air temperatures), some at regional scales (rainfall, solar radiation, climatic extremes, nutrient and acid depositions) and some at only local scales (hunting, land-use change; table 1). In addition, the drivers can be grouped as to the type of change. Both pan-tropical drivers (CO₂ and air temperatures) are point-change drivers, as

are rainfall and solar radiation (where a driver increases by Y at a point X where it was initially present). Land-use change is an extension-change driver (where a driver increases by Y at a point X where it was initially absent). All the remaining drivers mix both point and extension changes (table 1). Combining the scale at which changes are relatively uniform and the mode of change—point or extension—gives the extent of the expected changes in the driver. Thus, an extension-change driver that causes uniform changes at a local scale can have a near-global extent if that process, like increasing hunting pressure, is occurring over almost all areas of the biome. From the data available we can state that over the past two decades

- (i) air temperatures and CO₂ concentrations have increased globally at all locations;
- (ii) hunting and land-use change have increased globally, but not uniformly at all locations;
- (iii) rainfall, N deposition and O₃/acid depositions have changed regionally;
- (iv) there was no documented global increase in climatic extremes/ENSO events; and
- (v) incoming solar radiation may or may not have increased across many regions, but the diffuse : direct ratio probably has changed in some regions.

This exercise shows that rainfall, N depositions and O₃/acid depositions have only altered relatively consistently at a regional scale and are thus very unlikely to account for any widespread changes documented in tropical forests.

Different continents and regions are likely to be exposed to very different suites of changing drivers over the past two decades. Here, we draw attention to the main trends in the changes of drivers by continent, highlighting key differences (but see the following regarding uncertainties for some of these trends). Tropical South American forests are likely to have experienced

- (i) relatively high initial temperature, compared with tropical African forests, which are increasing;
- (ii) increasing CO₂ concentrations;
- (iii) no consistent rainfall trends;
- (iv) increasing solar radiation;
- (v) ENSO droughts, but with a strong spatial pattern running approximately northeast (strongly affected) to southwest (weakly affected) across the continent;
- (vi) relatively small increases in N deposition and O₃/acid depositions compared with tropical Asian forests; and
- (vii) the lowest levels of fragmentation of any continent.

African tropical forests, in contrast, are likely to have experienced

- (i) relatively low initial temperatures, which are increasing;
- (ii) increasing CO₂ concentrations;
- (iii) a strong trend of decreasing rainfall, which is rarely affected by ENSO droughts;
- (iv) relatively small increases in N deposition and

O₃/acid depositions, compared with tropical Asian forests;

- (v) very high levels of bushmeat extraction compared with tropical South American and Asian forests; and
- (vi) moderate levels of fragmentation compared with tropical Asia.

Asian tropical forests are likely to have experienced

- (i) higher temperatures than African tropical forests, which are increasing;
- (ii) increasing CO₂ concentrations;
- (iii) no overall trends in rainfall;
- (iv) a decrease in solar radiation, but an increase in the diffuse fraction owing to relatively higher air pollution compared with tropical African and South American forests;
- (v) high and rapidly increasing N deposition and O₃/acid depositions, compared with tropical African and South American forests; and
- (vi) highly fragmented and often intensively logged forest compared with the other continents.

Clearly, these broad differences between continents will contain regional variation. For example, Brazil's Atlantic forest—highly fragmented and near intensive agriculture and large industrialized areas—may experience drivers more similar to forests in Southeast Asia than much of the rest of tropical South America. Monitoring tropical forests across each of these continents and regions will be essential if we are to determine what changes are occurring across the biome, and to disentangle which potential drivers are causing any changes across the tropical forest biome.

(b) *Identifying uncertainties*

Few of the drivers we review have been directly measured across widespread areas of the tropics or shown to be altered unequivocally across most locations. Out of all the potential drivers we review, only air temperatures, rainfall and ENSO/climatic extremes are based on a large number of monitoring sites and multiple studies (IPCC 2001; New *et al.* 2001; Malhi & Wright 2004). Out of these, the increase in temperature is fairly consistent across the tropics, while the lack of a clear signal from ENSO events may be caused by high temporal variability as ENSO events may occur too infrequently to be able to detect trends over a few decades of measurements. The pan-tropical average decline in rainfall is mostly driven by strong spatial variability—the northern Congo Basin appears to be declining strongly in rainfall, whereas the rest of the tropics are showing little consistent change (Malhi & Wright 2004).

Clearly, there is a general lack of direct monitoring of the physical, chemical and biological environment across the tropics, beyond very basic climatic data. However, for some drivers there is good evidence of changes despite a lack of direct long-term monitoring. CO₂ is well mixed in the atmosphere, and thus does not need to be measured extensively across the tropics for one to be confident that CO₂ levels have increased and are increasing (IPCC 2001). Similarly, land-use change and hunting are well known to be proceeding apace, despite the challenges of

determining exactly how much change is occurring in particular areas. The largest gaps in our understanding concern monitoring changes in

- (i) solar radiation and cloudiness (Stanhill & Cohen 2001; Wielicki *et al.* 2002; Nemani *et al.* 2003); and
- (ii) chemical deposition, including N, P, tropospheric O₃ and various acid depositions (Fowler *et al.* 1999; Emberson *et al.* 2001).

There is consistent theory as to the *direction* of the impacts of most of the drivers, for example, that increasing CO₂ concentrations may increase growth rates, or that an increase in extreme climatic events may increase mortality rates (table 2). There is, however, ongoing debate about whether detectable increases in growth are expected from increasing CO₂ concentrations (Körner 2003; Clark 2004; Chambers & Silver 2004), or whether certain impacts are important when they do occur, as is the case with extreme but short-lived ENSO events in Amazonia (Sheil 1995; Williamson *et al.* 2000). For two potential drivers—air temperature increases and global dimming—there is a lack of consistency in the theoretically predicted direction of any changes that might occur in forests (table 1). Clearly, more experimental tests and observations are required in these two areas.

For no driver can we confidently predict that a change in the driver of the magnitude documented in this paper will cause a change in a given ecological process of a given magnitude. Experiments concerning these effects have, in the past part, not been conducted. Clearly, long-term experiments on mature old-growth forests are essential. Given the pivotal nature of tropical forests in the global C cycle and their likely contribution to the buffering and/or acceleration of the rate of climate change over the coming decades, experiments increasing CO₂ concentrations for whole stands of naturally growing trees, alongside nutrient addition experiments and air and soil warming experiments, are essential to reduce the enormous uncertainty in making predictions about tropical forests and their likely responses to various global changes.

(c) *Potential drivers and forest plot data*

Data from a network of long-term forest plots from across the tropical forests of South America (Malhi *et al.* 2002b) have shown increases in stem recruitment (Phillips *et al.* 2004), stem mortality (Phillips *et al.* 2004), and hence stem turnover, with recruitment exceeding mortality leading to an increase in stem density (Lewis *et al.* 2004). In addition, stand-level forest growth has increased, as has mortality on a stand-level biomass basis, and hence biomass turnover has increased (Lewis *et al.* 2004), with growth exceeding losses causing an increase in stand-level above-ground biomass (Baker *et al.* 2004). Overall, these forests appear to have become more productive, more dynamic and to hold more biomass. What driver or drivers may be causing this suite of simultaneous changes within these forest plots?

Considering this suite of changes in South American tropical forests, an environmental driver increasing mortality could not produce a net increase in above-ground biomass, so is unlikely to be driving changes in the dynamics documented. Similarly, a driver increasing recruitment

could not cause the observed increases in biomass losses from mortality, nor the increases in growth or net above-ground biomass by the amounts documented, as recruited stems are a very small proportion of total above-ground biomass and stem numbers. However, a driver that increases the levels of resource availability could cause an increase in stem growth and the other observed trends. Three environmental drivers may have increased resource availability across South America over the past 20 years and hence increased forest growth: temperature, solar radiation and CO₂ concentration increases.

Air temperatures and CO₂ have certainly increased, whereas more data on changes in solar radiation and cloudiness are needed to confirm the suspected increases in incoming solar radiation and possible shifts in direct and diffuse components. In addition, there is no consensus over whether CO₂ increases, air temperature increases or changes in solar radiation causing global dimming actually increase forest growth. Further analyses of forest plot data, data on solar radiation and experiments on the effects of temperature and CO₂ increases are required to move beyond our current working hypothesis that an increase in resource availability across South America is driving increases in NPP and hence increasing growth and accelerating forest dynamics.

Further tests may help to distinguish the three possible drivers and seven hypotheses for increasing resource availability and hence NPP. First, determining whether these trends are pan-tropical or are just occurring across one continent should be a research priority for ecologists. This requires expanding the network of plots, particularly across the Congo Basin and Borneo. Second, there are several potential tests to separate the different mechanisms. For example, the increase in incoming solar radiation across the tropics is likely to have a spatial pattern (Nemani *et al.* 2003). Southern Borneo, the wettest parts of West Africa and northern Queensland are all tropical forest areas where NPP has been predicted to decline. By contrast, northern Borneo, Central America, the central Congo Basin and most of Amazonia are predicted to have increased NPP over the 1980s and 1990s (Nemani *et al.* 2003). This spatial signature can be tested using long-term forest plot data. Likewise, examining spatial differences in background temperature, notably the generally lower temperatures in African forests, and any correlations between changes in stem growth and changes in temperature may be illuminating.

(d) *The future*

Under the simplest scenario of a steady rise in forest productivity over time, it is predicted that relatively slow-growing and undynamic forests would remain a C sink for a century or more (Chambers *et al.* 2001). However, the drivers documented in this paper will all change in the future, most probably causing further alterations in forest structure and dynamics. In general, the drivers expected to cause elevated *mortality* are very likely to increase, as

- (i) expected increases in climatic extremes are likely to increase tree mortality;
- (ii) increasing N deposition, O₃/acid deposition and other pollutants may increase tree mortality as

industrialization continues to spread across the tropics; and

- (iii) habitat fragmentation increases mortality rates in remaining forest.

In addition, the current increases in the rates of *growth* (apparently caused by year-to-year better conditions for growth) cannot continue indefinitely, as

- (i) if CO₂ is a cause, trees are likely to become CO₂ saturated at some point in the future;
- (ii) if the apparently large increases in incoming solar radiation are the cause, this is thought to be a decadal-scale oscillation, and thus will not continue into the medium term (Wielicki *et al.* 2002); and
- (iii) if temperature increases are the cause, points of inflection will more often be reached, decreasing net photosynthetic rates and C gains, and/or respiration costs will rise, both substantially reducing growth rates.

Finally, we predict increases in either stem recruitment and/or mortality rates under all 10 drivers (either directly or via effects on growth), so stem turnover rates are also very likely to continue to rise in the future. Overall, the future trends are likely to be further increases in stem mortality and recruitment rates, with mortality overtaking recruitment, leading to declines in stem density at an increasing number of sites. Simultaneously stand-level growth is expected to asymptote or decrease and biomass losses from mortality continue to rise. As a result stand biomass may well decrease in surviving old-growth forests well within the current century. While there is considerable uncertainty on the future trajectory of the drivers and the responses of tropical forests, the expected changes in the drivers plausibly predict that the current C sink contribution of mature tropical forests to buffering the rate of climate change is very likely to diminish and quite possibly reverse in the future (e.g. Cox *et al.* 2000).

The drivers of change we document can be grouped into four categories: those caused by

- (i) decadal-scale natural climatic oscillations;
- (ii) fossil fuel emissions and resulting climate change;
- (iii) increasing industrialization in the tropics; and
- (iv) the further integration of forest products and land into expanding national and international market economies.

To slow or halt widespread changes in remaining tropical forests will require large reductions in fossil fuel emissions, a different form of development in tropical countries than has occurred in temperate nations, and a minimum of carefully regulated markets. Under 'business as usual' conditions, rapid global changes will continue to alter the world's remaining tropical forests with global consequences for biodiversity, climate and human welfare.

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GLOSSARY

- ENSO: El Niño–Southern Oscillation
 LW: longwave
 NPP: net primary productivity
 NSC: non-structural carbohydrate
 Rubisco: ribulose biphosphate carboxylase
 TOA: top of atmosphere