Tropical forests and global warming: slowing it down or speeding it up?

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The world's tropical forests take up and emit large amounts of carbon (C) through photosynthesis and respiration. Their response to global changes in the atmosphere and climate could therefore act as a feedback. Only recently has research been focused on the possibility that tropical forests may not be in C balance. There is currently a vigorous debate about whether these ecosystems might be accelerating or slowing down the rate of atmospheric CO_2 accumulation, and thus global warming. The evidence is thin in either direction, and in some cases highly uncertain. Some findings raise the possibility that higher temperatures could make tropical forests increasing C sources to the atmosphere – a positive feedback effect. To project where our climate is headed, it is critical to resolve two questions: how tropical forests are reacting to changing climate, atmosphere, and land use, and how they will continue to respond over the coming decades.

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To many people, the mention of tropical forests conjures up images of vine-covered, buttressed trees, brilliant butterflies, and other examples of the rich biodiversity harbored in these ecosystems (Figure 1). For others it will bring to mind the worldwide crisis of tropical deforestation. Few will think of the pivotal role these forests could be playing in global climate change.

Recently, scientists have come to consider the possibility that tropical forests could be shifting their carbon (C) balance in response to the effects of anthropogenic greenhouse gas emissions. In one such view, even old growth tropical forests might be serving as a globally significant C sponge, responding to the increase in atmospheric carbon dioxide (CO_2) by growing more biomass and/or accumulating more C in the soil (Phillips *et al.* 1998; Mahli and Grace 2000; Prentice *et al.* 2001; Schimel *et al.* 2001). On the other hand, over the past two decades there has been remarkable variation in how much of each year's fossil fuel emissions actually stay in the atmosphere. Some recent findings suggest that these temporal swings in the rate of atmospheric CO_2 accumulation reflect negative impacts on tropical forest C balance in years of peak temperatures and drought (Keeling and Piper 2001; Rödenbeck *et al.* 2003; Clark *et al.* 2003). Do either of these inferences accurately represent general trends across the world's tropical forests? Which will prevail in the coming decades?

The answers to these questions have implications that go far beyond the forests themselves. These ecosystems process huge amounts of C every year – they have been estimated to account for 35% of global plant productivity (Saugier *et al.* 2001). If they currently take more C from the atmosphere than they emit, tropical forests are acting as brakes on the rate of global warming by decreasing atmospheric greenhouse gas content. If on the other hand they are now, or are soon to become, net C emitters, they could substantially accelerate the pace of global warming. The information we currently have is too limited to establish whether there is an imbalance between C uptake and emission by tropical forests and, if there is, in which direction. A review of this area of global change science shows how challenging it will be to quantify the current and future C fluxes of this key biome.

In a nutshell:

- Both tropical deforestation and shifts in tropical C balance affect atmospheric CO_2
- Both C uptake and C emission could change in response to the ongoing changes in our atmosphere and climate
- One possibility is that rising temperatures and intensified drought could outweigh any benefits in plant productivity from higher CO_2 levels
- If this occurs, tropical forests would become increasing net CO_2 sources

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Why is atmospheric CO_2 increasing?

It is first useful to review a simplified diagram of the global C cycle in the 1990s (Figure 2). The annual increase in atmospheric CO_2 is the net result of several large CO_2 fluxes to and from the atmosphere. Humans directly drive two of these: the emissions from fossil fuel combustion and cement production, and the net C added to the atmosphere by land-use change, principally due to tropical deforestation. Much larger quantities of C are moved into and out of the atmosphere by the world's oceans and terrestrial ecosystems. Neither the oceans nor the land-based ecosystems would affect atmospheric CO_2 if their C uptake exactly equaled their emissions. However, most analyses indicate that both the oceans

Figure 1. *View across the canopy of an old growth tropical rainforest at La Selva, Costa Rica.*

and the land have been acting as C sinks during the past two decades (Prentice *et al.* 2001; Keeling *et al.* 2001; Plattner *et al.* 2002; Rödenbeck *et al.* 2003).

Where do the numbers in Figure 2 come from? The atmosphere's CO_2 content, and thus its annual increase (Prentice *et al.* 2001), are measured based on global sampling. Annual fossil fuel and cement production emissions are thought to be reliably quantified by country-level statistics (Prentice *et al.* 2001). The estimated net flux from tropical land-use change is a new update (Houghton 2003a), and, as the author emphasized, involves considerable uncertainty. The values for C uptake and emissions by the oceans and terrestrial ecosystems are based on the most recent report of the Intergovernmental Panel on Climate Change (IPCC) (Prentice *et al.* 2001), with the emission estimates adjusted to reflect the range of net fluxes inferred in recent atmospheric analyses (Keeling and Piper 2001; Rödenbeck *et al.* 2003). Although estimates will probably change as our knowledge evolves, the diagram illustrates two robust points about the tropics. First, it is critical to quantify accurately the tropical deforestation C flux. Second, relatively small imbalances between photosynthesis and respiration by tropical ecosystems could also produce substantial net C emissions to the atmosphere.

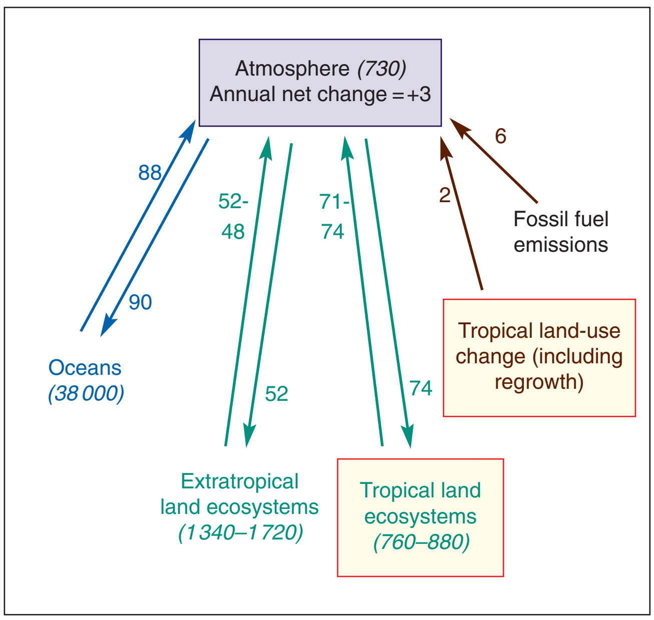

Figure 2. *The increase in atmospheric CO_2 each year is driven both by anthropogenic C emissions to the atmosphere (brown arrows) and by the net balances between the very large amounts of CO_2 that are taken up and emitted by the oceans (blue arrows) and the land (green arrows). Values are in petagrams (billions of tons) of C. Bold indicates annual fluxes (see text for sources), and italics indicates total estimated stocks (Prentice* et al. *2001).*

Net C emitted by tropical deforestation

It is easy to see how difficult it is to estimate this flux. No one has actually measured the C content of even one hectare of tropical forest. To do this, one would have to harvest, dry, and weigh hundreds of trees, vines, epiphytes, and other plants, including their roots, as well as all the dead wood and litter, and then analyze many soil samples from multiple depths. Instead, researchers use shortcuts such as empirical relationships between tree biomass and diameter, derived by laboriously harvesting and weighing a sample of trees at a few sites (Brown 1997). The C in litter, roots, and soils, which is rarely measured, is generally estimated based on very limited data from other sites. Further complicating the situation, old growth and different-aged successional forests vary greatly in their average wood density, tree height, and soil depth, and there are other vegetation types in the tropics, including grasslands, low shrublands, and savannas.

For each time interval, national deforestation statistics or satellite images are used to estimate how much area of each vegetation type was affected by human activities. Then estimates must be made of how much biomass was burned (Figure 3) or removed in logging, how much was left to decompose, and how fast it decomposes. Because these emissions from changing land use are a net figure, we also need estimates of how much new biomass was produced in the interval by plantations and by young, regrowing forests and other successional vegetation on altered lands.

There are other, potentially large changes in C stocks that are poorly quantified to date. When fire is used to clear and maintain tropical pasture, even mild fire incursions into adjacent forests can kill trees and predispose the stands to massive mortality from subsequent fires (Barlow *et al.* 2003; Cochrane 2003). Such damage is likely to be much more widespread than has been generally recognized (Nepstad *et al.* 1999). Another, less obvious C loss is the degradation of forest structure ("biomass collapse") that can occur in wide strips along the edges of fragmented forest (Laurance *et al.* 1998). Very large amounts of soil C can also be lost when tropical forests are converted to pasture (Veldkamp *et al.* 2003) or when exotic tree species are planted (Chapela *et al.* 2001).

Figure 3. *The clearing and burning of tropical forests – here seen in Novo Airão, Brazil – produces large C emissions to the atmosphere.*

Not surprisingly, the various estimates of total net C flux from tropical land-use change vary widely and are all highly uncertain (Houghton 2003b). A recent estimate for the 1990s of 2.2 Pg C/yr (1 petagram = 1 billion tons) was derived from country-level deforestation statistics (Houghton 2003a). Considerably smaller fluxes of 0.91 PgC/yr (Defries *et al.* 2002) and 0.96 PgC/yr (Achard *et al.* 2002) were inferred from two analyses of satellite images for 1990–1997. Although these smaller values are closer to each other, the underlying regional flux distributions differed, and Achard *et al.*'s (2002) estimate did not take into account forest degradation or soil C loss with land-use change; Houghton's (2003b) adjustments for these factors raise this estimate of the total net C flux from tropical land-use change to 1.3 PgC/yr. All three of these estimates are multi-year averages. Much greater net C fluxes from tropical deforestation are likely to have occurred in particular years of recent decades when political or socioeconomic conditions promoted land clearing, or when extremely hot and/or dry periods increased fire risk. During the exceptional 1997–1998 El Niño event, Page *et al.* (2002) estimated that 0.8–2.6 Pg C was emitted by the burning of peat swamp forests in Indonesia alone.

■ Tropical forest C balance

In addition to the net emissions from tropical land-use change, any imbalance between the very large amounts of C absorbed and emitted by tropical ecosystems (Figure 2) will affect atmospheric CO_2 accumulation. Our current understanding of plant ecophysiology indicates opposite ways that ongoing atmospheric and climate changes could be altering the tropical forest C balance.

Higher CO_2 levels might be expected to increase tropical forest productivity through commonly seen plant responses such as increased photosynthesis and water-use efficiency. Surprisingly, however, in the more realistic experiments where tropical plants have been exposed to elevated CO_2 (plant "communities" in growth chambers, field-rooted seedlings/saplings, in situ canopy branches), the general response has been a buildup of non-structural carbohydrates in leaves and twigs, and little or no growth enhancement (Clark in press; Körner in press). These few experiments have all been short-term (< 1.5 yr), however, and thus may not accurately indicate long-term forest responses to the continuing buildup of atmospheric CO_2.

Global warming might be expected to have strong negative impacts on the C balance of these already warm forests. Respiration by plants (Amthor and Baldocchi 2001) and microbes (Holland *et al.* 2000) increases exponentially with temperature. In contrast, photosynthesis increases with rising temperature to a peak rate (at the photosynthetic optimum temperature) and then declines rapidly (Baldocchi and Amthor 2001). For canopy-level leaves of trees and lianas measured in different tropical forests (Clark in press), the photosynthetic temperature optimum was found to be in the range 26–34°C; tropical forest canopy leaves are already often warmer than this. In addition, many tropical trees and lianas show greatly increased C losses in the form of volatile organic compounds when leaves are exposed to the higher temperatures that already occur in daytime hours (Geron *et al.* 2002). The peak-temperature years of recent decades also brought strongly decreased rainfall (Keeling and Piper 2001), and thus intensified drought stress, to many tropical forests. Nevertheless, a big unknown is whether processes such as photosynthetic acclimation or substrate limitation of respiration will moderate the forests' response to these ongoing changes.

We know very little about the effects of other potentially important factors. For example, tropical light levels could be changing. Increases in incoming radiation and tropical forest productivity in the past two decades were

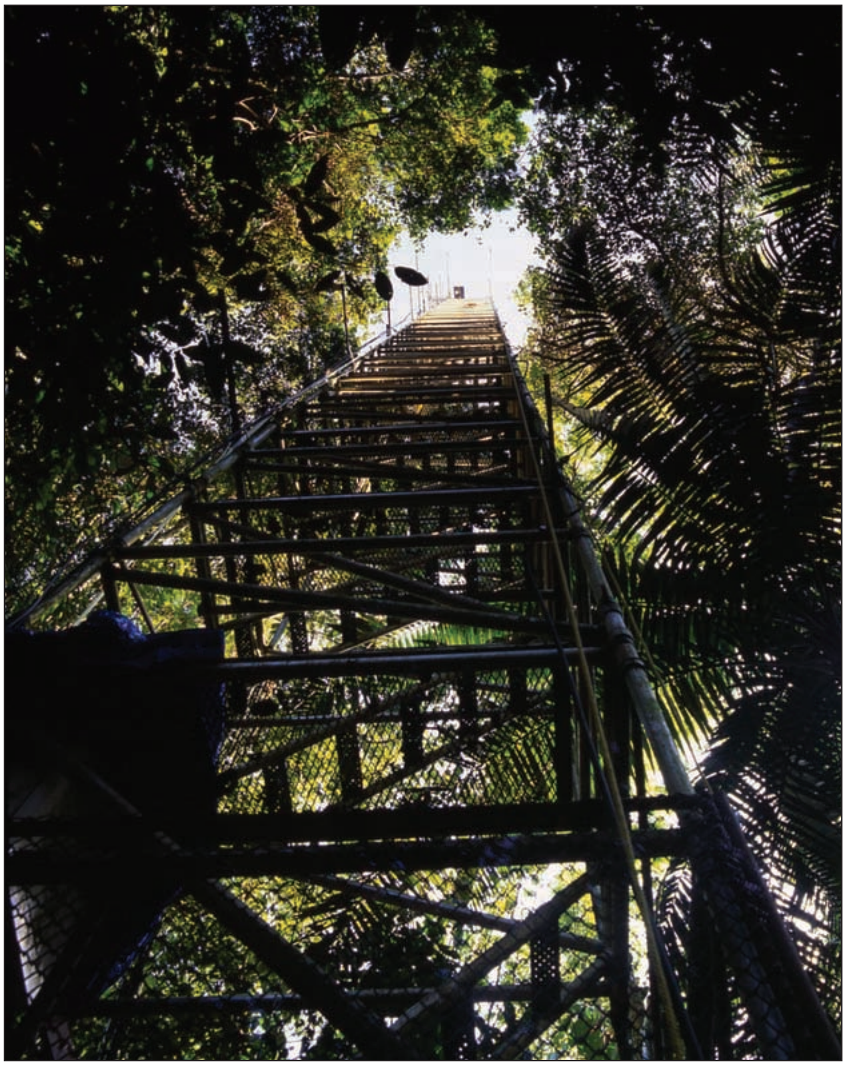

Figure 4. *Above-canopy towers, such as this one in the old growth lowland forest at La Selva, Costa Rica, are used for eddy covariance studies of whole-forest C balance.*

recently inferred, based on vegetation modeling and satellite data (Nemani *et al.* 2003). The radiation data (from a single satellite) have been questioned, however (Trenberth 2002), and the inferred increase in forest productivity has not been corroborated by field data. Another issue is nutrient limitation and possible changes in nutrient cycling. One modeling study suggests that anthropogenic nitrogen deposition could lead to important nutrient losses from tropical ecosystems (Asner *et al.* 2001). Unfortunately, there has been no long-term monitoring of tropical forest nutrient cycling.

In the real world, all these factors operate simultaneously. To determine the integrated response of tropical forests requires direct observations of ecosystem performance. The existing data, which were based on several different research approaches, are limited. As they have accumulated, however, the number of points of agreement among them appears to be increasing.

One focus has been historical trends in aboveground biomass of old growth tropical forests, as estimated by remeasurement of all the trees in a large number of forest inventory plots. A first analysis of such data from the past several decades indicated no forest biomass change in the Paleotropics, but a biomass increase in the Neotropics (Phillips *et al.* 1998). However, questions have arisen about the methods used in the Neotropical dataset (Clark 2002; Phillips *et al.* 2002). Recently, Baker *et al.* (in press) took another look, using a large Amazonian dataset which included many new plots and excluded many problematic ones. This analysis indicated no clear forest biomass change in the eastern and central Amazon plots. For upland western Amazon forests, the researchers estimated a significant biomass increase, noting that this estimate could be affected to an unknown degree by early measurement problems.

One unresolved issue is whether small, unreplicated plots accurately sample forest biomass trends. Even when a forest is in C balance at the total-landscape scale, most sites within an old growth forest are accumulating biomass, while the large C losses from natural disturbance tend to be sporadic and localized (Fearnside 2000; Körner in press). In the three cases where all the trees were remeasured over several years in many hectares of the same old growth tropical forest landscape (Laurance *et al.* 1997; Chave *et al*, 2003; Clark in press), the data indicated no change in aboveground biomass.

A second type of field evidence has come from eddy covariance studies of forest C exchange. This high-tech approach is based on measuring the movement and CO_2 content of the air above the canopy, using instrumentation at the top of a tall tower (Figure 4). The data are integrated over the study period to estimate the net CO_2 flux in or out of the forest. Early findings in two old growth forests of the Brazilian Amazon (Grace *et al.* 1995; Mahli *et al.* 1998) indicated substantial net C uptake. More recently, however, researchers have found that eddy covariance data from tropical forests can seriously underestimate nighttime respiration, because the air is often still at night (Mahli *et al.* 1998; Loescher *et al.* 2003; Saleska *et al.* 2003; Miller *et al.* in press). In two recent Amazonian eddy covariance studies where the data were filtered to minimize such effects, and where independent ground measurements were carried out as a cross-check, it was concluded that the forests were likely to have been net C sources during the study interval (Saleska *et al.* 2003; Miller *et al.* in press).

Inferences can also be made from long-term data on tropical tree growth and mortality. A 16-year record of annual tree growth in the old growth forest at La Selva, Costa Rica documents marked interannual variation (61–278% differences between years) in the diameter growth of diverse canopy tree species from 1984 to 2000 (Clark *et al.* 2003). Although the inter-year temperature range was only 1.75°C, these growth variations were temperature-related; the diameter increments were greatly reduced in the hotter years. Long-term data on tree mortality from tropical forests worldwide also show a link to high temperatures. In the mega-Niño events of 1982/3 and 1997/8, when both temperatures and drought were exceptional in many forests, researchers documented major increases in tree death in diverse tropical forests (Clark in press).

Table 1. Recent estimates of the annual average C flux between the terrestrial tropics and the atmosphere in the 1990s, as estimated from inversion calculations based on atmospheric data

When the estimated net C emissions due to tropical land-use change (column 2) are subtracted from this overall flux (column 1), the remainder (column 3) is an estimate of the C balance of tropical ecosystems. Units are petagrams (billions of tons) of C

Overal net tropical land flux		Net flux from tropical land-use change[1]	C balance of tropical ecosystems
-0.4 Pg C/yr (sink)[2]	=	+2.2 Pg C/yr (source)	-2.6 Pg C/yr (sink)
+2.6 Pg C/yr (source)[3]	=	+2.2 Pg C/yr (source)	+0.4 Pg C/yr (source)
+1.5 Pg C/yr (source)[4]	=	+2.2 Pg C/yr (source)	-0.7 Pg C/yr (sink)
-0.8 Pg C/yr (sink)[5]	=	+2.2 Pg C/yr (source)	-3.0 Pg C/yr (sink)

[1]Houghton 2003a [2]Summary of estimates for 1990–1994 (Schimel *et al.* 2001) [3]1990–1999 (Keeling and Piper 2001) [4]1992–1996 (Gurney *et al.* 2002, as adjusted by Houghton 2003b) [5]1996–1999 (Rödenbeck *et al.* 2003)

These limited whole-forest observations indicate little if any increase in aboveground biomass by old growth tropical forests in recent decades, and some of the findings point to negative impacts on these forests in the warmest years of this period. The existing forest-level data are inadequate, however, for establishing the forests' overall C balance and whether it has changed during the past decades. All the tropical forest eddy covariance studies have been short-term (<1 to 3 years), and none has been corroborated by on-site field assessments of the change in total forest C stocks. As noted above, there is no example of a tropical forest in which all the C, both above- and belowground, has been quantified. We therefore still lack the field observations required to assess whether tropical forests are in C balance.

Evidence from the atmosphere

At the global scale, inferences can be made from the spatial and temporal variation in atmospheric CO_2. The data from ongoing atmospheric sampling at a global network of stations can be analyzed to estimate global and regional C sources and sinks by a method known as an inversion calculation. Researchers first develop models of C emissions and uptake by all terrestrial ecosystems and the oceans, and combine them with fossil-fuel emission data and a model of global winds. The resulting atmospheric responses are then fit to the actual gas measurements. Such inversion calculations have been carried out on data for atmospheric O_2/N_2 or CO_2, sometimes taking account of the C isotopes ^{13}C and ^{12}C, for varying periods during the past two decades. In some calculations, the results are reported by latitude, allowing conclusions to be drawn about the net exchange of CO_2 between the terrestrial tropics and the atmosphere. As the authors of these studies (see Table 1) note, however, the calculations involve a great deal of uncertainty, especially for the tropics, where the atmospheric sampling stations are sparse and data on atmospheric transport are limited.

Recent inversion model estimates of the net flux from the tropical land regions during the 1990s run the gamut from net C uptake to net C emissions (Table 1). When adjusted by Houghton's (2003a) estimate of the flux due to tropical land-use change (see Figure 2), three of these studies indicate that tropical ecosystems were a moderate to strong C sink in the 1990s, while one study finds them to have been a net C source (Table 1).

There is more agreement, however, concerning the large year-to-year variation in how fast atmospheric CO_2 has increased. Annually resolved inversion analyses (Bousquet *et al.* 2000; Keeling and Piper 2001; Rödenbeck *et al.* 2003) indicate that the inter-year differences in atmospheric C dynamics have largely been driven by the C fluxes of land ecosystems, and that the tropics have played an important role. Tropical emissions have been inferred in years of peak temperatures and drought in the tropics (generally El Niño years). For the period 1984–2000, there is a remarkably close correspondence between the tropical terrestrial C fluxes inferred from one of these inversion calculations (Piper *et al.* 2001) and the record of annual tree growth in the La Selva rain forest (Clark *et al.* 2003). This is the first time findings from an atmospheric inversion calculation have been independently corroborated by long-term ground measurements of forest productivity.

In summary, therefore, analyses of atmospheric data from the past two decades have indicated that the terrestrial tropics have strongly influenced the temporal variation in atmospheric CO_2 accumulation, and that in years of higher tropical temperatures (generally associated with rainfall minima), the C balance of the land tropics has shifted in the direction of increased emissions. It is important to remember that these tropical emissions are the sum of three large fluxes: (1) C uptake through photosynthesis; (2) C emission by respiration of both plants and hetero-

Panel 1. What if old growth tropical forests become C sources?

If rising temperatures tip the respiration–photosynthesis balance of old growth tropical forests in the direction of net C emissions, the resulting positive feedback to atmospheric CO_2 accumulation would clearly be a global concern. Although it is perhaps counterintuitive, such a scenario would reinforce current mandates to conserve these ecosystems. Tropical forests store many hundreds of tons of C per hectare in their biomass and soil. Disruption of these stores through fires, clearing, or logging would produce much greater and much more immediate C releases than would an ongoing imbalance between uptake and emissions by protected old growth forests. A separate and fundamental reason to protect such ecosystems is their exceptional and irreplaceable biodiversity.

trophic organisms (principally microbes); and (3) the net emissions from tropical land-use change (Figure 2). As noted above, the 1997/98 mega-Niño event brought large C emissions from exceptionally large tropical fires, as well as high temperatures and drought that could shift the balance between C uptake and emissions by tropical ecosystems; both could have contributed to the large tropical C emissions detected over that time period by the inversion models. If tropical fires and other types of forest loss varied substantially between years in recent decades, they could be important in the interannual variation of tropical land C emissions. Furthermore, these fluxes are from all tropical vegetation types, including extensive grasslands and savannas. Both caveats notwithstanding, these atmospheric findings are consistent with the hypothesis that the responses of tropical forests to global warming are already affecting the rate of atmospheric CO_2 accumulation (Panel 1).

A research agenda

Temperatures and atmospheric CO_2 levels will continue to increase in the coming decades (Prentice *et al.* 2001; Albritton *et al.* 2001). Although it is by no means a certainty, one possibility raised by the evidence in hand is that the response of tropical forests to these ongoing changes will be a shift in C balance in the direction of emissions, producing a positive feedback to global warming. In line with this hypothesis, one modeling study (Cox *et al.* 2000) has projected massive mortality of tropical forests beginning a few decades from now, with a resulting large increase in atmospheric CO_2 levels by the year 2100.

How realistic is this scenario? The field data coming out of some major current research efforts will help answer this question. Teams of researchers, such as the RAINFOR network in the Amazon (Mahli *et al.* 2002) and the CTFS global plot network (Condit 1995), have been censusing tropical forest plots around the world at intervals of several years, to assess tree growth, mortality, and aboveground biomass. Over the long term, these studies will document any pronounced trends in tree dynamics and forest composition. The international Large-Scale Biosphere–Atmosphere program underway in the Amazon involves many types of research, including eddy covariance studies of forest C balance. In spite of this progress, however, the gaps in our current understanding of tropical forest C storage and fluxes around the globe remain dauntingly large (Panel 2).

There are several steps that could make a big difference. First, as emphasized by Houghton (2003b), we must refine our monitoring of tropical forest cover and intensify field research to decrease the large uncertainties regarding the biomass of tropical old growth, secondary forests, and other vegetation. We need to expand climate monitoring and add atmospheric sampling stations throughout the world's tropics. Multi-year studies of both above- and belowground C cycling are greatly needed in representative tropical forests; to date, measurements have been short-term and largely confined to aboveground wood production and litterfall. Annual data are needed on as many forest processes as possible, from tree growth and mortality to soil C cycling; how these processes vary with interannual climate variation could indicate longer term responses to climate change. The need to monitor tropical soil C stocks is critical – this C pool is huge and may be undergoing change. Finally, the two ongoing forest drydown experiments (eg Nepstad *et al.* 2002) need to be emulated in the form of forest-level experiments to test the effects of warming and increased CO_2 on tropical forest processes.

Fulfilling such a research agenda would go a long way towards resolving the open questions about how tropical forests may be shaping our future climate. At the same

Panel 2. Large knowledge gaps about tropical forest carbon stocks and fluxes

"The uncertainty on the tropical land region is large; lack of atmospheric data in this region means that inversion methods cannot reliably comment on the extent to which sources due to tropical land-use change are balanced by enhanced growth." (Gurney *et al.* 2002)

"The current lack of adequate data on land-use change and ecosystem processes for the tropics makes it impossible to evaluate ground-based versus atmospheric estimates as is done for the northern extratropics." (Schimel *et al.* 2001)

"The current lack of an adequate monitoring program to measure changes in forest cover in the tropics is remarkable. Such a monitoring program, using high-resolution satellite data over the last three decades and into the future, would probably do more to constrain the tropical and global net terrestrial flux of carbon than any other measurement." (Houghton 2003b) time, we need to effectively communicate to policy makers and the public what we know with certainty and what we can infer about possible future trends. What science and society at large do about these global issues now will have important consequences for the future of tropical forests and our climate.

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