

Tropical forests and atmospheric carbon dioxide

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Tropical forests play a major role in determining the current atmospheric concentration of CO₂, as both sources of CO₂ following deforestation and sinks of CO₂ probably resulting from CO₂ stimulation of forest photosynthesis. Recently, researchers have tried to quantify this role. The results suggest that both the carbon sources and sinks in tropical forests are significantly greater than previously thought.

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The inexorable rise of atmospheric CO₂ concentrations, as observed at Mauna Loa since the 1950s, is perhaps the most familiar scientific graph of the 20th century^{1,2}. It sits as indisputable evidence that human activity is modifying the earth's atmosphere at a global scale and is at the centre of the debate on global climate change. The cause of this rise is well understood; CO₂ is being emitted through the large-scale burning of oil, coal and gas, which power modern industrial economies, with an additional contribution coming from the clearing of tropical forests and woodlands. However, these changes are meshed within an immense natural global carbon (C) cycle that is still poorly understood and that will almost certainly provide new surprises. Here, we focus on the role that tropical forests play in this global CO₂ exchange.

Tropical forests occupy a broad band girdling the earth's moist equatorial regions, occupying approximately $17\,560 \times 10^3$ km² in 1990 (Ref. 3). Using the definitions and estimates of the Food and Agriculture Organization (FAO)³, these regions include lowland evergreen rainforests (7180×10^3 km²) at the equator, moist deciduous forests (5870×10^3 km²), dry deciduous forests (2380×10^3 km²), and hill and montane forests (2040×10^3 km²). In total, tropical forests and woody savannas account for 50% of global forest area. These biomes are characterized by high productivity – a recent model⁴ estimated that the annual net carbon production of tropical forests is 18 Pg C (1 Pg = 10¹⁵g) and that of savannas is 17 Pg C; in total, accounting for 60% of global terrestrial photosynthesis.

The principal components of the atmospheric CO₂ cycle can be summarized as follows:

$$E_{\text{ff}} + E_{\text{trop}} = \Delta_{\text{atm}} + \Delta_{\text{ocean}} + (\Delta_{\text{trop}} + \Delta_{\text{other}})$$

$$5.5 \pm 0.5 \quad 1.6 \pm 1.0 \quad 3.3 \pm 0.2 \quad 2.0 \pm 0.8 \quad 1.8 \pm 1.6$$

The values shown in this equation are the often quoted mean values for 1980–1989 in Pg C year⁻¹; they represent the state of knowledge of the Intergovernmental Panel on Climate Change (IPCC) in 1995 (Refs 2,5). E_{ff} is the rate of CO₂ emission through fossil fuel combustion and cement production, E_{trop} represents tropical deforestation, Δ_{atm} is the observed increase in atmospheric CO₂, and Δ_{ocean} , Δ_{trop} and Δ_{other} are the net sequestration into the oceans, the tropical terrestrial biosphere and other components of the terrestrial biosphere, respectively. E_{ff} and Δ_{atm} can be estimated with reasonable accuracy, but the other terms have greater uncertainty attached; in particular, the terrestrial biosphere sink has often been calculated as a residue of the other terms. A great deal of research effort has gone into quantifying these terms more effectively; here, we will focus on recent thinking regarding the magnitude of E_{trop} and Δ_{trop} – the terms relevant to tropical forests.

A case study of the tropical forest carbon cycle

The C dynamics of a forest are dominated by the assimilation of CO₂ through gross photosynthesis (G_p); the release of C through autotrophic (plant) respiration, R_a ; the transfer of C to the soil in the form of leaf, wood and root litter, and the exudation of organic compounds into the rhizosphere⁶; and the eventual release of this soil C back to the atmosphere through decomposition and respiration by microbes and other heterotrophs (R_h). There are few tropical sites where the internal forest C cycle has been examined in detail. Figure 1 shows a case study from a dense lowland tropical forest, with no history of disturbance, near Manaus in central Amazonia, Brazil. G_p and R_t were calculated directly from continuous measurements of CO₂ exchange above

the forest canopy, using the micrometeorological technique of eddy covariance^{7,8}. Recently, this technique has been applied to tropical forests^{7,9,10}, and has begun to produce a flood of information on the C balance of tropical forests and its relation to climatological variables.

Of the G_p of 30.4 t C ha⁻¹ year⁻¹, approximately 14.8 t C ha⁻¹ year⁻¹ are respired through leaves, wood and roots; the remainder (15.6 t C ha⁻¹ year⁻¹) is termed the net primary production, N_p . This C is fixed into plant structural biomass before eventually being deposited into the soil in the form of litter, dead trees or animal faeces, from where it is eventually released by microbial decay. The mean residence time of C in biomass and soil can be estimated by dividing the respective C stocks by N_p . The above-ground biomass stocks were measured directly (C is approximately 48% of dry biomass¹¹), the belowground biomass was assumed to be 33% of aboveground biomass¹² and soil organic C stocks were derived from other studies in Amazonia¹³.

We estimated the mean C residence times to be 16 years in biomass and 13 years in soils, totalling to 29 years¹⁴. Figure 1b shows a simplified version of Fig. 1a. There is a net transfer of CO₂ into biomass at a rate of 15.6 t C ha⁻¹ year⁻¹. This C remains in the biomass for a mean residence time of 16 years, at which time it is transferred to the soil where it remains for 13 years before being returned to the atmosphere.

The value of N_p suggested here exceeds the usual values of 6–14 t C ha⁻¹ year⁻¹ derived from field allometric studies^{15,16}. However, it is now widely recognized that almost all N_p estimates in the literature are low because root turnover and exudation have usually been ignored¹⁷. Aboveground growth and respiration can account for only a fraction of the total G_p ; there has to be a significant transfer of C belowground to bring consistency to forestry and gas-exchange measurements. If fine root turnover and exudation are neglected in our calculation, then $N_p = 9.8$ t C ha⁻¹ year⁻¹ – within the usual range. Is our estimate for belowground C cycling realistic? The few direct studies in temperate trees⁶ indicate that between 40% (for *Liriodendron tulipifera*) and 73% (for *Pinus sylvestris*) of assimilated C is transferred belowground to roots and to mycorrhizae; in Fig. 1a it is 45% for a tropical forest, a fairly conservative value compared with these temperate studies.

Whatever their exact magnitude, it seems certain that belowground C flows are a significant, and often underestimated, component of N_p . Thus, the value

of 18 Pg C year⁻¹, quoted earlier for global tropical forest productivity, might be an underestimate; 25 Pg C year⁻¹ might be closer to the true figure.

Carbon emissions from tropical deforestation: E_{trop}

The three principal zones of tropical forest are in South America, central Africa and southeast Asia. All three areas are undergoing rapid deforestation, primarily because of clearing for croplands (55%) or cattle pasture (20%), or because of the expansion of logging and shifting cultivation (12% each)¹⁸. Table 1 shows the extent of tropical forests in 1990 (Ref. 3), and the rates of clearance between 1980–1990 and 1990–1995 (Ref. 19). The Americas account for over 50% of tropical forest area, and the absolute clearance rates are highest here. However, relative clearance rates are highest in tropical Asia. Although they are still high, deforestation rates appear to have diminished by 12% in the 1990s.

Table 1 shows two recent estimates of net C emissions from tropical land-use change. Both estimates use data on annual land-use change, and stocks of C in biomass and soil to estimate the release of CO₂ at the time of ecosystem disturbance. Houghton¹⁸ attempted to calculate annual C emissions from forest and soil, by tracking the decay and regrowth of C stocks in the years and decades following disturbance; however, Fearnside²⁰ expresses C loss as net committed emissions (the total amount of C lost as the landscape approaches a new equilibrium). If deforestation rates are approximately constant, the two values are approximately equivalent.

Houghton's results are essentially an update of those used to provide the IPCC 1995 value for E_{trop} of 1.6 ± 1.0 Pg C year⁻¹, but they now include a revised and detailed analysis of tropical Asia²¹, which has increased the estimate

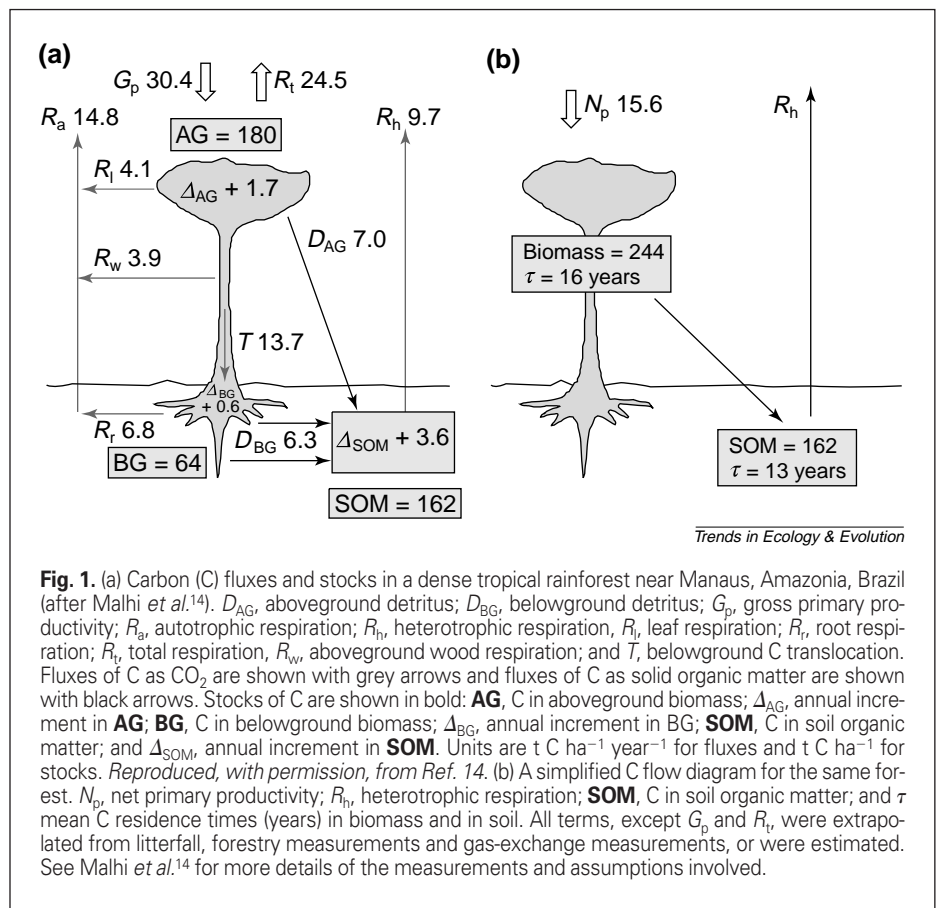


Fig. 1. (a) Carbon (C) fluxes and stocks in a dense tropical rainforest near Manaus, Amazonia, Brazil (after Malhi *et al.*¹⁴). D_{AG} , aboveground detritus; D_{BG} , belowground detritus; G_p , gross primary productivity; R_a , autotrophic respiration; R_h , heterotrophic respiration; R_l , leaf respiration; R_r , root respiration; R_t , total respiration; R_w , aboveground wood respiration; and T , belowground C translocation. Fluxes of C as CO₂ are shown with grey arrows and fluxes of C as solid organic matter are shown with black arrows. Stocks of C are shown in bold: **AG**, C in aboveground biomass; Δ_{AG} , annual increment in **AG**; **BG**, C in belowground biomass; Δ_{BG} , annual increment in **BG**; **SOM**, C in soil organic matter; and Δ_{SOM} , annual increment in **SOM**. Units are t C ha⁻¹ year⁻¹ for fluxes and t C ha⁻¹ for stocks. *Reproduced, with permission, from Ref. 14.* (b) A simplified C flow diagram for the same forest. N_p , net primary productivity; R_h , heterotrophic respiration; **SOM**, C in soil organic matter; and τ mean C residence times (years) in biomass and in soil. All terms, except G_p and R_t , were extrapolated from litterfall, forestry measurements and gas-exchange measurements, or were estimated. See Malhi *et al.*¹⁴ for more details of the measurements and assumptions involved.

of mean 1980s emission in that region from 0.7 ± 0.3 to 1.1 ± 0.5 Pg C year⁻¹. Fearnside's study is centred on a detailed analysis for Brazilian forest and savanna¹², which is based on a regional evaluation of C stocks, field studies of forest burning and satellite-derived deforestation rates.

These new studies significantly increase the estimated 1980s value of E_{trop} to about 2.0 Pg C year⁻¹, but in different regions and for varied reasons. In the final column in Table 1, we suggest a current 'best estimate' for C emissions in the 1980s, by combining the new analyses for the Americas²⁰ and Asia²¹, and

averaging the results for Africa. This now pushes the estimated emissions from tropical deforestation to 2.4 ± 0.6 Pg C year⁻¹. However, even this might be an underestimate, because several recent studies have suggested that human activity induces significant biomass reduction in apparently intact forests that is not accounted for in current analyses. Fearnside estimated that a further 0.4 Pg C year⁻¹ are emitted through forest degradation. A field survey²² of wood mills estimated that forest impoverishment through logging contributes an additional 4–7% to the net C release through Amazonian deforestation, and leaves the

Table 1. Deforestation rates and estimated resulting CO₂ emissions in tropical areas^a

Region	Forest area ^b (10 ³ km ²)	Moist forest area ^c (10 ³ km ²)	Deforestation rate ^a 1980–1990 (10 ³ km ² year ⁻¹)	Deforestation rate ^a 1990–1995 (10 ³ km ² year ⁻¹)	Carbon emission Houghton ^a (Pg C yr ⁻¹)	Carbon emission Fearnside ^a (Pg C yr ⁻¹)	Carbon emission combined ^d (Pg C yr ⁻¹)
Americas	9179.2	8705.1	64.8	56.9	0.55	0.94	0.94
Africa	5275.9	3730.2	41.9	37.0	0.29	0.42	0.36
Asia	3106.0	2663.7	39.7	35.1	1.08	0.66	1.08
Total	17561.0	15098.9	146.4	129.0	1.90	2.00	2.40

^aDeforestation rates 1980–1990 and 1990–1995, taken from Ref. 18. Houghton's estimates of carbon (C) emissions taken from Ref. 19 and Fearnside's estimates of C emissions taken from Ref. 20.

^bIncorporates rainforest, moist deciduous forest, dry and very dry forest, hill and mountain forest, and alpine area forest, as defined by the Food and Agriculture Organization (FAO)³.

^cIncorporates only rainforest, moist deciduous forest, and hill and mountain forest, as defined by the FAO (Ref. 3).

^dEstimate for C emissions in the 1980s by combining the new analyses for the Americas²⁰ and Asia²¹, and averaging the results for Africa.

Table 2. Net carbon (C) balance and implied biotic C sink in tropical forest regions^a

Region	Net balance ^a Rayner <i>et al.</i> (Pg C year ⁻¹)	Net balance ^a Bousquet <i>et al.</i> (Pg C year ⁻¹)	Net sink ^b Rayner <i>et al.</i> (Pg C year ⁻¹)	Net sink ^b Bousquet <i>et al.</i> (Pg C year ⁻¹)
Americas	-0.2	0.1	-1.1	-0.8
Africa	+0.0	0.2	-0.4	-0.2
Asia	-0.1	0.8	-1.2	-0.3
Total	-0.3	1.1	-2.7	-1.3

^aThe net C balance as inferred from analysis of atmospheric concentrations of CO₂. The Rayner *et al.* estimate is taken from Ref. 27; and the Bousquet *et al.* estimate of net C balance is taken from Ref. 28.
^bThe implied biotic C sink, calculated by subtracting our best estimate of CO₂ emissions from deforestation (last column of Table 1) from the estimates of net C balance (Columns 2 and 3, above).

forest vulnerable to ground fires²³ that have the potential to more than double total C emissions in dry years. In addition, much of the surviving forest, adjacent to areas of deforestation, is fragmented²⁴ and, thus, prone to biomass loss even in the absence of human harvesting²⁵.

These recent studies suggest that it is not implausible that the true rate of CO₂ emission through tropical deforestation in the 1980s might have approached 3.0 Pg C year⁻¹, almost double the value reported by IPCC in 1995 (Ref. 5). If so, one question begs an answer: where is this extra C going?

CO₂ in the tropical atmosphere

An independent view on terrestrial C emissions can be obtained by examining the temporal and spatial variation of CO₂ concentrations in the atmosphere. Recent studies have attempted to provide continental-scale maps of the distribution of C sinks and sources²⁶⁻²⁸. There are small gradients in mean atmospheric CO₂ concentration between hemispheres and between continents, caused primarily by the uneven spatial distribution of surface C sources and sinks, and by relatively slow mixing by the troposphere. In principle, if the global distribution of CO₂ concentrations and fossil fuel emissions, and the global transport and dispersion rates estimated from meteorological models, is known, the models can be inverted to provide a spatial surface map of CO₂ sources and sinks. Monitoring the ratios ¹³C:¹²C and O₂:N₂ can provide further information on the relative partition of the fluxes between oceans and terrestrial biosphere^{29,30}. However, there are several methodological difficulties with this approach¹⁴, including insufficient long-term CO₂ concentration records, difficulties in assessing tropospheric CO₂ concentrations from near-surface measurements³¹ and the problem being poorly constrained mathematically. The tropics

are a particularly difficult region in which to carry out such an analysis because there are few CO₂ sampling sites³², and because the intensity of tropical convection results in vigorous mixing and dilution of any spatial patterns of CO₂ concentration³¹. Such problems should diminish as the distribution and accuracy of CO₂ sampling stations improves.

Table 2 presents results from two recent analyses of atmospheric CO₂ distribution. Rayner *et al.*²⁷ used global CO₂ measurements over the period 1980-1995, and a long-term record of ¹³C:¹²C and O₂:N₂. Bousquet *et al.*²⁸ analysed CO₂ concentrations over the period 1985-1995. The two results disagree significantly both in the spatial distribution of CO₂ sources and sinks, and in the net tropical balance. Rayner *et al.*²⁷ suggest a modest net sink in the terrestrial tropics, whereas Bousquet *et al.*²⁸ suggest a significant net source concentrated in southeast Asia. There are still several inconsistencies with this approach.

Commentaries on these results usually focus on the C sink in temperate regions. Perhaps this reflects the geographical bias of the scientific research community. Also, it is not always emphasized that these atmospheric techniques should find a large CO₂ source in tropical latitudes, of the magnitude indicated by the deforestation studies - neither of these studies does so. This feature encapsulates the debate surrounding the C balance of tropical forests: studies of deforestation indicate that tropical regions are releasing large quantities of CO₂, but only some, or none, of this CO₂ is measured in the tropical atmosphere. There are several possible reasons for this discrepancy:

- The deforestation studies strongly overestimate the net C release accompanying land-use change.
- The atmospheric transport models underestimate the mixing of CO₂

between low and mid-latitudes, and, thus, underestimate how quickly the tropical CO₂ signature is dissipated.

- There is a large CO₂ sink in the terrestrial tropical biosphere.

Working on the third assumption and using the 'best estimate' of tropical deforestation in Table 1, the third and fourth columns in Table 2 show the magnitude of the C sink that would be required in each region to bring consistency between deforestation and atmospheric studies. The implied sink is significant and is probably distributed across all three continents. Is such a C sink plausible?

A tropical carbon sink: Δ_{trop}

The net C budget of an area of forest is the balance between net production and heterotrophic respiration. As shown in Fig. 1b, these two terms must be in approximate balance because any change in N_p eventually produces a corresponding change in R_h, with a lag time equal to the sum of the soil and the biomass residence times. For example, if there is a short-term increase in R_h, because of an increase in soil temperature, the soil C stocks will eventually decrease to bring R_h back to a level with N_p. However, variations in N_p and R_h on a timescale shorter than the residence time can result in a net flux of C to or from the forest system. Thus, interannual variation in cloudiness, precipitation and temperature might result in significant interannual variations in forest C balance³³.

There is also probably a longer term shift superimposed on this interannual variation. Mean atmospheric CO₂ concentration has increased from a pre-industrial value of 280 ppm to 366 ppm in 1998 (Ref. 1), and is currently increasing at about 1.5 ppm year⁻¹. A recent review of experimental studies growing trees in open-top chambers³⁴ indicates that a 300 ppm increase in atmospheric CO₂ concentration stimulates photosynthesis by 60%, the growth of young trees by 73% and wood growth per unit leaf area by 27%. It seems probable that there will be a similar response in natural forest ecosystems. Because of their intrinsic high productivity, tropical forests are a prime candidate for such a C fertilization response³⁵; the crucial question has been to what extent such a response might be limited by low nutrient availability, in particular by low nitrogen or low phosphorus. Several studies have attempted to model the effect of rising CO₂ on tropical forest productivity, with the magnitude of the resulting increase being largely dependent on how the nutrient cycle is modelled^{36,37}. Recently, it has been argued that forests might simply

Table 3. The net biotic carbon (C) sink in tropical regions

Region	0.1% year ⁻¹ increase ^a (Pg C year ⁻¹)	0.3% year ⁻¹ increase ^a (Pg C year ⁻¹)	Eddy covariance ^b (Pg C year ⁻¹)	Forest biomass ^c (Pg C year ⁻¹)	Forest soil ^c (Pg C year ⁻¹)	Forest total ^c (Pg C year ⁻¹)
Americas	-0.41	-1.22	-2.6	-0.62	-0.53	-1.14
Africa	-0.17	-0.52	-1.1	-0.26	-0.23	-0.49
Asia	-0.12	-0.37	-0.8	-0.19	-0.16	-0.35
Total	-0.71	-2.12	-4.5	-1.1	-0.9	-2.0

^aThe estimated net C sink resulting from rates of increase of net primary productivity of 0.1% year⁻¹ and 0.3% year⁻¹.

^bThe net C sink extrapolated from the mean sequestration rate measured by eddy covariance studies (see text).

^cThe net C sink in forest biomass is extrapolated from forest biomass data; the sink in forest soils is estimated from soil C residence times (see text); and the total C sink is the sum of biomass and soil C estimates.

increase their nutrient acquisition processes by investing in mycorrhizal colonization, and by mineralizing nutrient reserves in the soil by the production of surface enzyme systems and organic acid exudates³⁸.

A small steady increase in forest productivity can produce a large net C sink. For a linear increase in N_p , followed by a linear increase in respiration with lag time τ , the rate of C sequestration is $\tau \cdot dN_p/dt$ (Ref. 39). Using the forest areas in Table 1 and making the assumption that the values of N_p and τ presented in Fig. 1b are representative of the entire tropical forest biome, the C sink resulting from increases in forest productivity of 0.1% year⁻¹ and 0.3% year⁻¹ is calculated in Table 3. The result is a simple extrapolation and should be treated with caution, but it does demonstrate how a small increase in productivity can generate a significant C sink.

A terrestrial tropical C sink of 2.0 Pg C year⁻¹ is equivalent to a per unit area sink of 1.1 t C ha⁻¹, if distributed evenly across the tropical forest biome. If genuine, such a rate of C increase should be

directly measurable at the surface. In recent years, an increasing amount of field research has attempted to directly measure this C sequestration.

One approach has been to directly measure the CO₂ exchange above tropical forests, using the eddy covariance technique mentioned previously. This is a high-technology, equipment-intensive measurement – thus far only three field results have been reported. A short study in central Amazonia⁹ in 1987 suggested an annual sequestration rate of 2.2 t C ha⁻¹ year⁻¹; a medium-term study in southern Amazonia¹⁰ in 1993 estimated a C sink of 1.0 t C ha⁻¹ year⁻¹; and a year-long study in central Amazonia⁷ in 1995–1996 calculated a net C sequestration of 5.9 t C ha⁻¹ year⁻¹. The last study is the same as that demonstrated in Fig. 1. Eddy covariance techniques provide a vast amount of data on the temporal variation of C balance from hourly to annual timescales, but their spatial extrapolation is hampered by the high costs involved and the few results currently available. In the past year, there has been a proliferation of eddy covariance

studies in tropical forests, primarily as part of the LBA (Large Scale Biosphere–Atmosphere Experiment in Amazonia) experiment in Brazil [LBA Science Plan (1999) <http://www.cptec.inpe.br/lba/>], but also in Costa Rica and southeast Asia.

However, a lingering concern is that micrometeorological techniques might not be fully measuring CO₂ respired at night and, therefore, might be overestimating the net C sink. There is vigorous ongoing debate and research on this issue^{40–42}. A further possibility is that C leaks out of the forest in forms that are not usually measured, such as gaseous emissions of hydrocarbons^{43,44} or dissolved C in groundwater flows⁴⁵. These are thought to be relatively small, but surprises cannot be ruled out. Table 3 plots the mean tropical forest sink calculated by averaging the three eddy covariance studies and multiplying this by the area of wet tropical forest in each biome. The total predicted tropical C sink is 4.5 Gt C year⁻¹, the largest suggested by any of the calculations in this article. This seems implausible unless there are ‘missing sources’ in the global C budget that are currently neglected.

An alternative approach to detecting C uptake has been the examination of long-term forestry plots for evidence of an increase in biomass. A recent study⁴⁶ compiled data from forest inventories across 68 sites in apparently undisturbed tropical forests. It found large variability between plots, but reached a remarkable conclusion – most South American forests have increased in biomass in recent decades and have been accumulating C in biomass at a rate of 0.71 ± 0.39 t C ha⁻¹ year⁻¹. In African and Asian forests, there appeared to be no net increase in biomass, but too few plots were analysed to be confident of this conclusion. Assuming that soil respiration rates have not been increasing, we can estimate the rate of accumulation of C in soils by multiplying the biomass sequestration rate by the ratio of the residence times

Box 1. Conclusions

- The productivity of tropical forests might be higher than previously estimated when below-ground productivity is fully taken into account.
- Recent studies suggest that CO₂ emissions from tropical deforestation and degradation might be significantly greater than previously estimated, perhaps even approaching 3.0 Pg C year⁻¹.
- Studies of the distribution of atmospheric CO₂ find either no tropical source or only a modest source, in spite of the large CO₂ efflux from deforestation, thus indicating the presence of a tropical sink of 1–3 Pg C year⁻¹.
- Forestry plot studies have indicated that the biomass of old-growth tropical forests has been increasing over recent decades, absorbing C into biomass at a rate of 1.1 Pg C year⁻¹. This might be a response to rising atmospheric CO₂ concentrations. If soil C changes are taken into account, the probable sequestration rate is 2.0 Pg C year⁻¹; however, this might be reduced if soil respiration rates increase in response to climatic warming.
- There is some degree of consistency between deforestation, forestry plot and atmospheric studies, suggesting a tropical C sink of 2.0 Pg C year⁻¹, a deforestation source of 2.4 Pg C year⁻¹ and a net tropical source of 0.4 Pg C year⁻¹. These values suggest that tropical productivity is increasing by approximately 0.3% year⁻¹ or 0.2% for every 1 ppm rise in CO₂ concentration.
- Micrometeorological studies are currently limited in number, but suggest a C sequestration rate that seems larger than plausible.
- On a continental scale, there is a surprising degree of consistency between sink estimates from the combination of atmospheric and deforestation studies, and those from the extrapolation of forest plot data.

$\tau_{\text{soil}}/\tau_{\text{biomass}}$ (Fig. 1b), thus arriving at a value of 0.61 t C ha⁻¹ year⁻¹ for soils or a total sequestration rate of 1.30 t C ha⁻¹ year⁻¹. The net sequestration rate in each tropical region can be calculated by multiplying this rate by the area of forest (Table 3). This includes the assumption that the low increase measured in Africa and Asia reflects paucity in data rather than a genuine difference between regions, thus the mean uptake rate calculated for South American forests can be applied to all three regions. The calculation suggests a total tropical forest sink of 2.0 Gt C year⁻¹, half of which is in South America.

On a continental scale, there is a surprising degree of consistency between these sink estimates, and between those obtained from the combination of atmospheric and deforestation studies. Both approaches indicate a sink of about 1 Pg C year⁻¹ in the Americas and a smaller sink in the less extensive African forests. However, in Asia Rayner *et al.* indicate a much larger sink than seems plausible given the small relative area of Asian tropical forests. This suggests a problem either with the results of Rayner *et al.* or with Houghton's C source estimate for Asia.

Is a global tropical forest sink of 2.0 Gt C year⁻¹ consistent with recent studies of CO₂ fertilization and is it sustainable? Table 3 indicates that forest productivity would need to increase by 0.3% year⁻¹ as CO₂ concentrations rise by 1.5 ppm year⁻¹. If sustained, this implies a 60% increase in productivity for a 300 ppm increase in CO₂ concentration. This result seems consistent with experimental observations³⁴. However, in natural, as opposed to experimental, conditions, the trees form dense canopies that compete with each other and the stimulation of growth might be less. Perhaps a realistic estimate of the enhancement of productivity, taking into account competition by calculating the annual biomass increment per unit of leaf area, is about 30%. Thus, there appears to be an inconsistency between the magnitude of the tropical C sink suggested here and the results from laboratory studies of CO₂ fertilization.

A revised global carbon budget?

In this perspective, we have examined recent developments in the study of the productivity and C balance of tropical forests, with any eye to converging on a consistent picture of the tropical forest C sink. Such a consistent picture has not yet emerged, but there have been several major new developments. Our main conclusions are listed in Box 1.

It seems probable that tropical forests are greater sources and sinks of C

than previously estimated. We can suggest tentative revisions to the global C budget for the 1980s presented at the start of this article:

$$E_{\text{ff}} + E_{\text{trop}} = \Delta_{\text{atm}} + \Delta_{\text{ocean}} + \Delta_{\text{trop}} + \Delta_{\text{other}}$$

5.5±0.5	2.4±0.6	3.3±0.2	2.0±0.8	2.0	0.4
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Several studies have suggested substantial C sinks at mid and high latitudes^{47,48}, and, therefore, the 0.4 Pg C year⁻¹ ascribed to Δ_{other} is probably too small. This suggests that either E_{trop} is still being underestimated or Δ_{trop} is being overestimated. There are still significant error margins and further revisions to this budget are inevitable.

Future directions

The research areas reviewed here can all be expected to make significant progress over the next decade. There will be a substantial expansion of data sets in all fields, but methodological issues must still remain a focus of research.

For studies based on global atmospheric CO₂ concentrations, there needs to be an expansion of data points in poorly monitored regions, including tropical oceanic and continental regions, and improvements in the modelling of global trace gas transport, particularly between the tropics and the mid-latitudes.

For eddy covariance and other micrometeorological studies, the key question will be to explain the high C uptake rates currently being measured in tropical forests. Recently initiated field studies will provide a substantial data set, but attention still needs to be focused on unresolved methodological issues.

Long-term tropical forest plots offer great potential for direct monitoring of aboveground C stocks. There will be a substantial expansion of available data when all historical long-term forest plot records are compiled; however, these historical data sets will have several statistical and methodological problems. A more rigorous approach will be the establishment of large plots specifically tailored for research into long-term change, such as the 50 ha plots within the Centre for Tropical Forest Science network [<http://www.si.edu/organiza/centers/stri/forest/ctfs/start.html>].

The final point of convergence will be when field studies, laboratory studies and physiological models converge on a consistent picture of the C balance of each biome. This article has hinted at convergence between these diverse fields; we are optimistic that a more consistent picture of the net C balance of tropical forests, and of other biomes, will emerge over the next decade.

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The nature of predation: prey dependent, ratio dependent or neither?

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To describe a predator–prey relationship, it is necessary to specify the rate of prey consumption by an average predator. This functional response largely determines dynamic stability, responses to environmental influences and the nature of indirect effects in the food web containing the predator–prey pair. Nevertheless, measurements of functional responses in nature are quite rare. Recently, much work has been devoted to comparing two idealized forms of the functional response: prey dependent and ratio dependent. Although we agree that predator abundance often affects the consumption rate of individual predators, this phenomenon requires more attention. Disagreement remains over which of the two idealized responses serves as a better starting point in building models when data on predator dependence are absent.

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The rate of prey consumption by an average predator is known as the functional response; this can be classified as: (1) prey dependent, when prey density alone determines the response; (2) predator dependent, when both predator and prey populations affect the re-

sponse; and (3) multispecies dependent, when species other than the focal predator and its prey species influence the functional response. Until recently, predation theory was dominated by prey-dependent models and by Holling's¹ three-type classification of these re-

sponses. Arditi and Ginzburg² stimulated recent interest in alternative forms for functional responses with their suggestion that a ratio-dependent functional response was a better starting point for modeling predation. Ratio dependence is a particular type of predator dependence in which the response only depends on the ratio of prey population size to predator population size, not on the absolute numbers of either species. Figure 1 illustrates a prey-dependent response and a comparable ratio-dependent response.

The publication of Arditi and Ginzburg's suggestion received both support and criticism^{3–7}. The question underlying the debate is: how does predator population density influence the average predator's consumption rate? The answer to this question has an important influence on when and why predator–prey systems fluctuate, how they are likely to evolve and how they respond to environmental changes. The debate has persisted for more than a decade, in part, because ecologists know pitifully little about the nature of functional responses. Following prey-dependent theory, early empirical work typically measured the number of prey eaten by single predators in small cages⁸. This design eliminates the possibility of seeing anything other than prey dependence. Observations of