

Jean Pierre H. B. Ometto · Antonio D. Nobre  
Humberto R. Rocha · Paulo Artaxo · Luiz A. Martinelli

## Amazonia and the modern carbon cycle: lessons learned

Received: 2 July 2004 / Accepted: 28 January 2005 / Published online: 30 March 2005  
© Springer-Verlag 2005

**Abstract** In this paper, we review some critical issues regarding carbon cycling in Amazonia, as revealed by several studies conducted in the Large Scale Biosphere Atmosphere Experiment in Amazonia (LBA). We evaluate both the contribution of this magnificent biome for the global net primary productivity/net ecosystem exchange (NPP/NEE) and the feedbacks of climate change on the dynamics of Amazonia. In order to place Amazonia in a global perspective and make the carbon flux obtained through the LBA project comparable with global carbon budgets, we extrapolated NPP/NEE values found by LBA studies to the entire area of the Brazilian Amazon covered by rainforest. The carbon emissions due to land use changes for the tropical regions of the world produced values from 0.96 to 2.4 Pg C year<sup>-1</sup>, while atmospheric CO<sub>2</sub> inversion models have recently indicated that tropical lands in the Americas could be exchanging a net 0.62 ± 1.15 Pg C year<sup>-1</sup> with the atmosphere. The dif-

ference calculated from these two methods would imply a local sink of approximately 1.6–1.7 Pg C year<sup>-1</sup>, or a source of 0.85 ton C ha<sup>-1</sup> year<sup>-1</sup>. Using our crude extrapolation of LBA values for the Amazon forests (5 million km<sup>2</sup>) we estimate a range for the C flux in the region of –3.0 to 0.75 Pg C year<sup>-1</sup>. The exercise here does not account for environmental variability across the region, but it is an important driver for present and future studies linking local process (i.e. nutrient availability, photosynthetic capacity, and so forth) to global and regional dynamic approaches.

**Keywords** Amazonia · Carbon cycle · Deforestation · Climate changes

---

Communicated by Jim Ehleringer

J. P. H. B. Ometto (✉) · L. A. Martinelli  
Laboratório de Ecologia Isotópica—CENA/USP,  
Av. Centenário, 303, 13416-000 Piracicaba,  
SP, Brazil  
E-mail: jpometto@cena.usp.br  
E-mail: martinelli@cena.usp.br

A. D. Nobre  
INPA escritório de representação no INPE,  
Instituto Nacional de Pesquisas da Amazonia,  
Av. dos Astronautas, 1758 São José dos Campos,  
SP, 12227-010 Brazil  
E-mail: anobre@ltid.inpe.br

H. R. Rocha  
Departamento de Ciências Atmosféricas, Instituto Astronômico,  
Geofísico e de Ciências Atmosféricas, Universidade de São Paulo,  
Rua do Matão 1226, 05508-900, São Paulo, SP, Brazil  
E-mail: humberto@model.iag.usp.br

P. Artaxo  
Instituto de Física, Universidade de São Paulo, Rua do Matão,  
Travessa R, 187 05508-900, São Paulo, SP, Brazil  
E-mail: artaxo@if.usp.br

---

### Introduction

The sources and magnitudes of the major drivers of the global carbon cycle have changed since the beginning of last century, when the atmospheric carbon dioxide concentration started to rise consistently due to global emissions from fossil fuel and biomass burning (Schimel 1995). In the last few decades, a series of studies started to lay out the processes that could account for the fate of this additional carbon introduced into the atmosphere. However, the sum of fossil fuel and biomass burning emissions is higher than the balance of the carbon dioxide accumulated in the atmosphere and absorbed by the ocean and terrestrial biomes (Houghton et al. 1998). This budget mismatch between global sources and sinks, initially called “the missing carbon sink”, led to years of arguments about where the unaccounted sink could lie. Some hypotheses considered that the oceans could take more carbon dioxide than originally thought (Bousquet et al. 2000; Tans et al. 1990; Conway et al. 1994; Ciais et al. 1995). Others considered that the missing carbon was taken up by terrestrial ecosystems, via photosynthesis, but there were considerable difficulties in calculating precisely how much (Fan et al. 1998).

Additionally, global modeling studies have also calculated an increase in the rate of atmospheric CO<sub>2</sub> accumulation throughout the past century (Cox et al. 2000; Ito and Oikawa 2000; White et al. 2000).

The tropical rain forest biome plays an important role in the global carbon budget (Melillo et al. 1993; Dixon et al. 1994; Field et al. 1998), but there is great uncertainty about the ecosystem's current and future impact on atmospheric CO<sub>2</sub> accumulation (Tian et al. 2000; Schimel et al. 2001; Cox et al. 2000). There is no clear understanding of how the carbon balance of tropical forests responds to rapid, on-going changes in climate and atmospheric composition (Gash et al. 2004). In addition, more studies relating the role of nutrient limitation, such as nitrogen and phosphorus, to ecosystem carbon uptake (Vitousek 1984; Vitousek et al. 1986; Chadwick et al. 1999) are needed. Based on the records of atmospheric CO<sub>2</sub> concentrations and carbon isotope ratios (<sup>13</sup>CO<sub>2</sub>), Townsend et al. (2002) suggested a sizable terrestrial carbon sink in tropical latitudes for a period from 1991 to 2000.

Climate forcing, such as changes in precipitation (Marengo et al. 2001) and radiation (Procópio et al. 2004) also play a key role on future carbon exchange scenarios. With continuing global warming, significant changes in water regimes could influence carbon budget in tropical forests (Victoria et al. 1998; Malhi and Wright 2004). A better understanding of the nonlinear and complex integrated effects of nutrients, climate, and hydrology on carbon cycling is needed to improve global process models being used to project future atmospheric CO<sub>2</sub> levels and climate (Prentice et al. 2001; Cox et al. 2000).

Since the 1980s, there was a large increase in tropical deforestation followed by biomass burning. The carbon dioxide released from this burning has become critical for the global carbon balance equation. The role of the Amazon region, the largest continuous area of tropical forest in the world, came to the foreground in the global carbon quest. Several studies began estimating the area and rate of deforestation. The use of different remote sensing techniques to calculate the extent of the deforested areas produced heated controversy (Fearnside 1996), but considerably improved our understanding of the magnitude and rates of this process in this region (Fearnside 1997; Houghton et al. 2000). The average deforestation rate for the nineties was 17,000 km<sup>2</sup>·year<sup>-1</sup>, increasing to approximately 25,000 km<sup>2</sup> in 2002 and 2003 (INPE 2004). By 2004, an estimated of 16.32% of the total Brazilian Amazon area (5.8 million km<sup>2</sup>) will be deforested (INPE 2004). Most of this process is concentrated in the southern and eastern part of Amazonia, while the central, less accessible areas, are relatively protected. However, recent government plans for paving roads and developing infrastructure (Laurance et al. 2001), associated with increasing presence of highly capitalized agribusiness companies, threat central areas in a very near future (Soares-Filho et al. 2004).

Our understanding of the probable fate of the "missing" carbon had progressed considerably towards

the end of the 1990s, with evidence indicating that secondary forest regrowth in temperate forests was contributing to the terrestrial C sink. Also, extensive field studies, mainly in temperate terrestrial ecosystems, and large scale atmospheric surveys, associated with modeling efforts, indicated that the actual atmospheric carbon dioxide concentration, combined with excess nitrogen deposition, could be fertilizing ecosystems and increasing the carbon uptake through photosynthesis (Schimel 1995; Tans et al. 1998). However, the precise location and magnitude of these sinks remained unknown. This led to several studies focusing on the potential distribution of terrestrial sinks (Friedlingstein et al. 1995; Melillo et al. 1996; Thompson et al. 1996; McGuire et al. 1997). Due to their high biomass density, tropical forests were a natural candidate for a large sink component. Several modeling studies clearly supported this hypothesis (Friedlingstein et al. 1995; Melillo et al. 1996; Thompson et al. 1996; McGuire et al. 1997). Therefore, Amazonia was considered to be a potentially significant player in the global carbon cycle as either a sink or source, mainly due to the large amount of carbon stored in its biomass and large annual fluxes from photosynthesis, respiration, decomposition and fire.

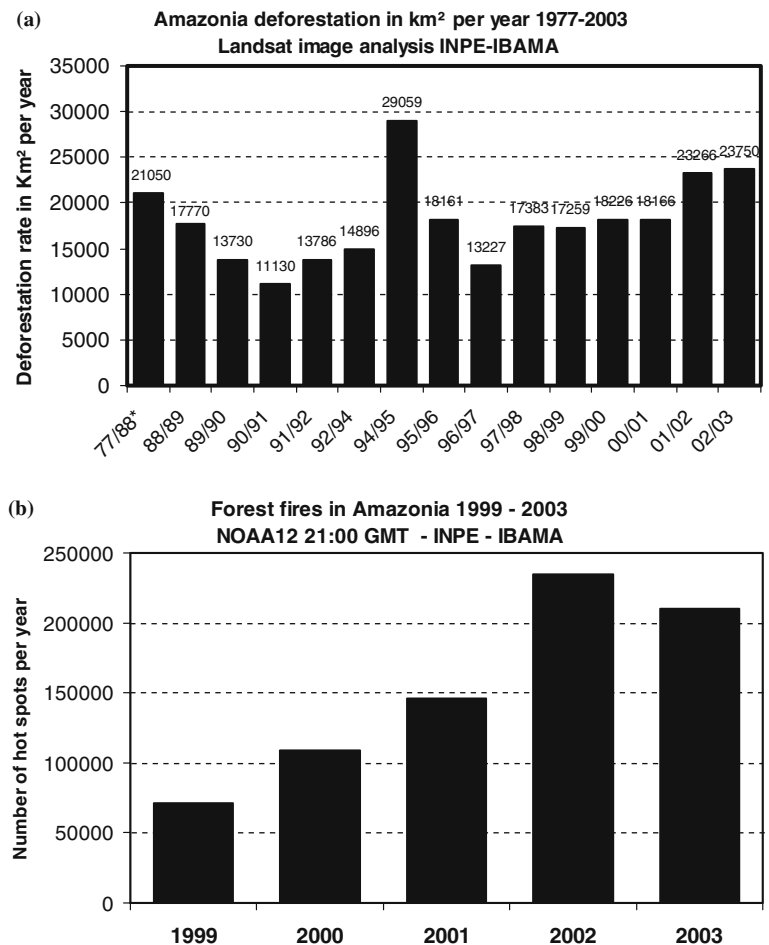
The Brazilian scientific community realized that it was time to develop a large integrated program devoted to studying ecological functioning of the Amazon region, especially considering its role in the modern carbon cycle. This was promptly supported by American and European colleagues. In 1997, the Large Scale Biosphere–Atmosphere Experiment in Amazonia (LBA), a Brazilian-led, multinational study of the interactions between the Amazonian region and the global climate system, was officially launched. Two major questions drove LBA investigations: (1) how does Amazonia currently function as a regional entity? (2) how will changes in land use and climate affect the biological, chemical, and physical functions of Amazonia, including the sustainability of development in the region and the influence of Amazonia on Global climate? (<http://lba.inpa.gov.br/lba>)

The long-lasting ecological paradigm, that mature tropical forests should be at climax, i.e. over time the net gain of carbon should near zero, presumed the existence of a dynamic mass balance in old growth forests. However, the first conclusive direct measurements of ecosystem CO<sub>2</sub> exchange conducted in Amazonia using eddy covariance technique (Grace et al. 1995a, b; 1996; Malhi et al. 1998), suggested a large net carbon uptake of 1–6 t C ha<sup>-1</sup> year<sup>-1</sup>. Therefore, the presumption of mass balance in primary forests was under question. These first measurements led to the speculation of whether pristine Amazon forests could be functioning as a giant carbon sink. An unforeseen sink in the tropical forests of the world, and in Amazonia in particular, could resolve the geographical mystery of the missing carbon sink. However, many researchers were skeptical about the magnitude of the sink predicted by these early eddy flux data. As a result, an intense review of the eddy

covariance method, including the applicability of scaling from the measuring site to the region, was initiated. This ongoing review has already pointed to difficulties in measuring CO<sub>2</sub> emissions in the very stable atmosphere that develops in tropical forests (Kruijt et al. 2004; Baldocchi et al. 2000), and shown large local heterogeneity of ecosystems (Araujo et al. 2002; Saleska et al. 2003). In parallel, a large effort in compiling long-term biomass changes in forest stands across the Amazon and around the tropical world sought to ascertain the sink or source status of carbon in primary forest vegetation (Phillips et al. 1998). These efforts were not yet clarified beyond doubt the overall role of Amazonia as a sink or source.

The main objective of this paper is to provide a critical overview of facts and uncertainties, and raise potential implications of what we have learned so far regarding the role of Amazonia in the modern carbon cycle. We will start with a review of the extent of deforestation in Amazonia, including estimates of how much carbon was released into the atmosphere through land use changes. This will be followed by a review of methods used to estimate the net ecosystem exchange (NEE) in the region, and ecological implications of the estimates found thus far.

**Fig. 1 a** Deforestation rate in the Brazilian Amazonia in Km<sup>2</sup>·year<sup>-1</sup>. Analysis using Landsat images by INPE/IBAMA (<http://www.inpe.br>). **b** Number of hot spots in Amazonia, from 1999 to 2003. Data obtained by INPE/IBAMA using the satellite NOAA 12, passing over Amazonia at 21:00 GMT



processes (see Hecht 1993; Margulis 2003; Nepstad et al. 2002; Walker and Moran 2000; Andersen et al. 2002). Road construction in pristine areas, cattle ranching, logging and agriculture are the main economic activities leading to deforestation (Nepstad et al. 2001). Recently, Hirsch et al. (2004) proposed the carbon and land-use change (CARLUC) model and calculated a cumulative carbon release to the atmosphere due to deforestation of  $\sim 7$  Pg C for the period from 1970 to 1998 in the Brazilian Amazon. This expansion of deforested areas reflected a large population increase in the region, from about 100,000 in 1840 to 1.5 million in 1940, up to about 18 million nowadays (Instituto Brasileiro de Geografia e Estatística, IBGE; <http://www.ibge.gov.br>, Brazil), with more than 50% of people living in villages and cities (Browder and Godfrey 1997).

According to measurements based on satellites images (<http://www.inpe.br>) the deforested area in the Brazilian Amazon was approximately 600,000 km<sup>2</sup> in August 2002. The Instituto Nacional de Pesquisas Espaciais (INPE) defines deforestation as “the conversion of primary forest areas by human activities for the development of agriculture and/or cattle ranching activities, as detected by orbiting satellites”. Another way to measure the deforested area is through ground-based land surveys done by IBGE Agricultural Census in Brazil. Andersen et al. (2002) presented an interesting comparison between these two methods. Estimations of deforested areas were generally larger based on surveys than when estimated by satellite data, probably because satellites detect gross deforestation and whereas surveys record the net deforestation, taking into account the regrowth of secondary forests (Andersen et al. 2002; Margulis 2003). Most of the deforestation occurs in primary forests, with grasses as the main replacing vegetation. Margulis (2003) suggested that planted pastures covered approximately 70% of the deforested area in Amazonia. Considering that fallow areas are used also for pasture, this estimate increase to almost 90%. It is also a consensus that most of the deforestation occurs along roads (Nepstad et al. 2001; Carvalho et al. 2001). Chomovitz and Thomas (2001) have calculated that

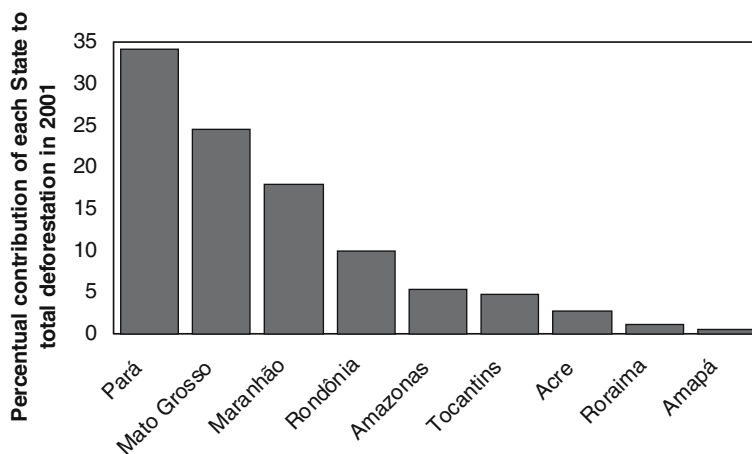
75% of all deforestation occurred within a 25 km-wide swath along the roads.

The first deforestation survey was carried out by INPE in 1977, and the second 10 years later (1988), after which annual surveys were performed. For the period 1977–1988, the average deforestation rate was close to 21,000 km<sup>2</sup> year<sup>-1</sup> (Fig. 1). In the subsequent years, this rate dropped to a minimum of 11,000 km<sup>2</sup> year<sup>-1</sup>, increasing again and reaching a record of almost 30,000 km<sup>2</sup> year<sup>-1</sup> in 1994/1995. For several years thereafter the rates decreased and stayed relatively constant, at around 17,000–18,000 km<sup>2</sup> year<sup>-1</sup>, increasing again to 25,000 km<sup>2</sup> year<sup>-1</sup> in the 2001–2003 period (Fig. 1b).

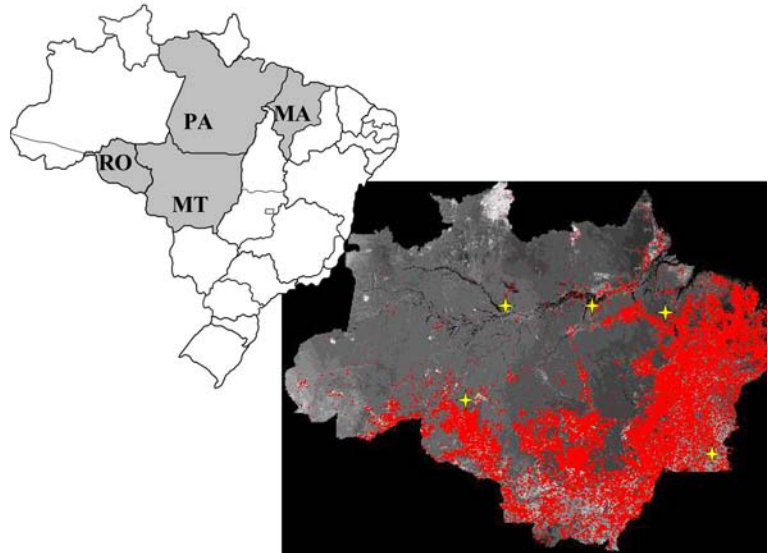
Four States of the so-called Brazilian Legal Amazon were responsible for more than 80% of deforestation (Fig. 2). One of the explanations for this trend lies in the greater exposure of the forest in its eastern and southern fringes to access from northeastern and southern regions of Brazil. Policies for occupation and development established by the military government in the 1970s and 1980s generated several destructive actions in the forest. Nowadays, the State of Mato Grosso has the biggest gross agricultural production in Brazil. In Pará and Maranhão States the expansion of soy bean agriculture is pushing cattle ranching still further into the forests. Road construction and paving have also allowed a fast expansion of deforestation in Rondônia and Acre.

Satellite observations of local regions of heat, or ‘hot spots’, created by the burning of cleared vegetation, are used as a proxy for deforestation in the region (Fig. 3) (<http://www.inpe.gov.br>). Maranhão State showed the lowest deforestation rates (Fig. 4), most likely because the bulk of deforestation in this State occurred prior to the start of monitoring in 1977. The highest rates of deforestation were observed in Mato Grosso State, mainly after 1990/1991 (Fig. 4), although the largest deforested area is located in Pará State. During the 1994/1995 burning season, the largest deforestation rate was observed indicating that, whatever caused this peak, it was a phenomenon observed all over the region (Fig. 4) (<http://www.inpe.gov.br>).

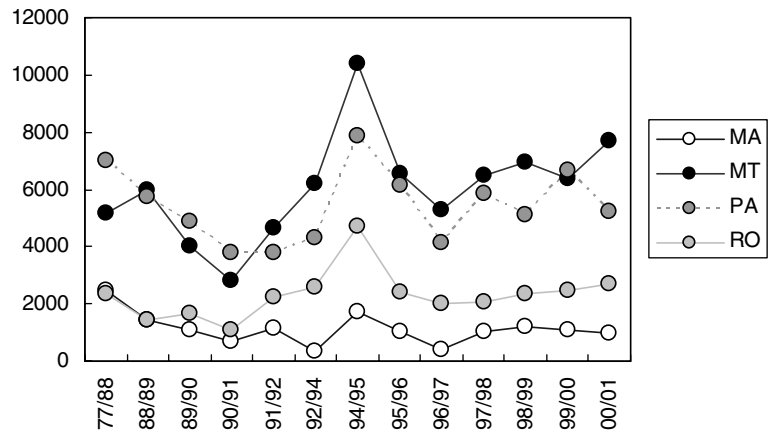
**Fig. 2** Percentage contribution of each State to total deforestation in the Brazilian Legal Amazonia region in 2001 (<http://www.inpe.br>)



**Fig. 3** Lower panel a satellite image of Brazilian Legal Amazonia with focus of heat in the 1998 burning season (<http://www.ibama.gov.br>). The stars markers indicate eddy covariance towers sites. Upper panel map of Brazil with State divisions. In gray the four states where deforestation is more intense



**Fig. 4** Deforestation rates in the four main States of the Brazilian Amazonia region. These four States contributes with more than 80% of deforestation in the region (<http://www.inpe.br>)



Estimates of deforestation provide only one component to assess carbon emissions. One also needs to know the standing biomass and the fraction of biomass released through burning immediately and also slowly over time. The difficulties and uncertainties of biomass estimates in tropical forests will be discussed in a later section of this article. Here, we will only summarize the available information in order to illustrate our lack of knowledge on quantifying this parameter, and how it affects estimates of carbon emissions.

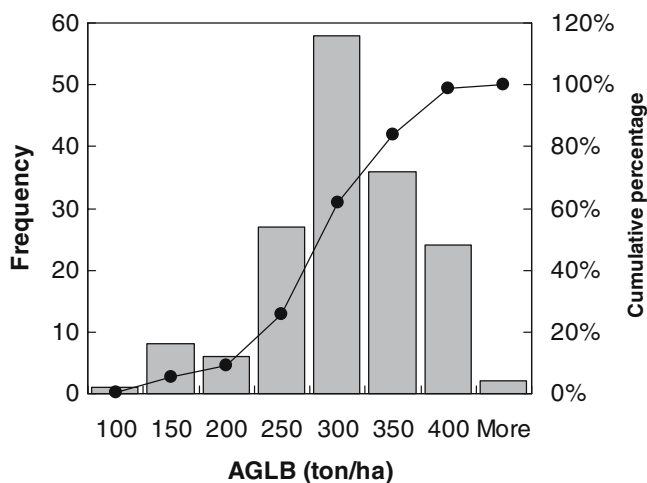
Houghton et al. (2001) summarized 44 sites in Amazonia where biomass was measured. They found a range of above-ground live biomass from 95 ton ha<sup>-1</sup> to 413 ton ha<sup>-1</sup>. One year later, Chambers et al. (2001b) made one of the most popular allometric equation available for the Amazon basin. This equation was obtained in central Amazonia, near the city of Manaus by harvesting 315 trees distributed in five plots of 0.04 ha each. This equation and others were used by

Baker et al. (2004a, b) to estimate the above-ground biomass in 59 forest sites. They found values varying from 124 ton ha<sup>-1</sup> to 320 ton ha<sup>-1</sup> across several transects. Houghton et al. (2001) summarized data from seven different biomass estimates for the Brazilian Amazonian forest and showed an average of 269 ± 86 ton ha<sup>-1</sup>. The original biomass estimate by Baker et al. (2004a, b) found 282 ± 57 ton ha<sup>-1</sup>, approximately 4% lower than the average value determined for measurements conducted 7–10 years later, at the same plots (294 ± 55 ton ha<sup>-1</sup>). Pooling both data sets together, the average of aboveground biomass in Amazonia can be estimated as 283 ± 66 ton ha<sup>-1</sup>. The frequency distribution of the aboveground biomass estimates can be seen in Fig. 5. Houghton et al. (2001) also summarized estimates for aboveground dead biomass and below ground biomass (live and dead not distinguished), representing 9% and 21% respectively of the total forest above ground live biomass. Therefore, adding 30% (accounting for dead



and below ground biomass) to the living aboveground biomass the estimated average for the total ecosystem biomass would yield from 126 ton ha<sup>-1</sup> to 537 ton ha<sup>-1</sup> in the Amazonian forests.

Considering the rates of deforestation between 1988 and 1998, the total biomass of Brazilian Amazonian forest, and the amount of carbon stored in the re-growing vegetation, it was possible to estimate the annual emission of carbon to the atmosphere. The average flux for this period was 0.18 ± 0.08 Pg C year<sup>-1</sup> (Houghton et al. 2000). If one accounts for logging activities and natural fires, the range of emissions can be calculated as 0.10–0.40 Pg C year<sup>-1</sup> (Houghton et al. 2000). This range would account for approximately 15–65% of the higher estimates of carbon emission for Tropical Latin America in the 1990s (0.62 Pg C year<sup>-1</sup>), and for 7–30% of the upper estimates of carbon emission for tropical areas globally (1.62 Pg C year<sup>-1</sup>) for the same period (DeFries et al. 2002). The global emissions due to land-use changes varies from 1.4 Pg C year<sup>-1</sup> to 3.0 Pg C year<sup>-1</sup>, considering the last estimate of 2.18 Pg C year<sup>-1</sup> made by Houghton (2003), the land-use change in Amazonia would be responsible for approximately 5–20% of global emissions. The Amazon region (~7.0 million km<sup>2</sup>) covers an area equivalent to 4.7% of the terrestrial area of the planet (150 million km<sup>2</sup>). Assuming that deforestation has already burned approximately 9% (0.6 million km<sup>2</sup>) of the region implies that an area equivalent to approximately 0.40% of the planet should be responsible for a significant share of the global carbon emissions due to land-use changes.



**Fig. 5** Frequency (left axis) and cumulative percentage distribution of aboveground live biomass. Data included 44 sites summarized by Houghton et al. (2001) and 59 sites summarized by Baker et al. (2004). The data from Baker et al. (2004) included the original measurement made 7–10 years ago and also the most recent biomass measurement

## Indirect effects of Amazonian deforestation on atmosphere composition and land–atmosphere carbon exchange

Changes in atmospheric composition—radiation and precipitation

Deforestation affects the atmosphere in several ways. First, there is a change in the energy and water balance when forest is replaced by pasture and this change has the potential to alter the atmospheric water content and precipitation patterns (Silva Dias et al. 2002). Second, when forests are cut and burned, large amount of particles and reactive trace gases are released into the atmosphere. This can lead to profound changes in the atmospheric composition (Andreae et al. 2002).

Most global circulation models simulated a decrease in the precipitation over Amazonia as a result of deforestation (Marengo and Nobre 2001), but these models have a very coarse resolution, and local processes and interaction between the land and atmosphere due to heterogeneity of the landscape cannot be properly assessed. New high-resolution mesoscale models were used to investigate the impact of land use change in Amazonia (Avissar et al. 2002), and they also simulated a decrease in precipitation due to deforestation. However, one recent study suggested that deforestation in portions of the region can lead to locally increased precipitation (Baidya Roy and Avissar 2002). This raises the hypothesis that there is a threshold of extent and distribution deforestation that leads to a precipitation decline (Avissar et al. 2002).

In addition to changes in the overall amount of precipitation, models have demonstrated that the patterns of precipitation over Amazonia are changing due to deforestation. Under forested conditions, low concentrations of aerosol particles prevail in Amazonia and a maritime-type cloud regime is formed in the region (Williams et al. 2002). This phenomena inspired atmospheric scientists to nickname Amazonia as the ‘green ocean’ (Andreae et al. 2004). Due to biomass burning, the aerosol concentration increased abruptly in some regions of Amazonia (Artaxo et al. 2002).

It is becoming clear that the Amazonian ecosystem is very sensitive to global climate forcing agents such as El Niño, regional changes in precipitation patterns and global warming (Marengo and Nobre 2001). Fire risk is among those sensitive to climate, but fire is also affected by management (Nepstad et al. 2001). The potential for fire to spread from deforested areas into fragmented forests represents a threat to long-term ecosystem health and sustainability (Cochrane et al. 1999; Cochrane and Laurance 2002). Logging thins the canopy, increases sunlight penetration to the understory and facilitates burning of the forest floor. After an Amazonian forest stand burns once, the reduced canopy cover and increased penetration of solar radiation increases the probability that fire will be able to spread through the

stand again (Cochrane et al. 1999). The interactions of climate, management and fire susceptibility produce several mechanisms of positive feedback that may lead to further forest degradation, fire risk, and negative economic and human health consequences (Nepstad et al. 2001).

### Emissions of volatile organic carbon

Tropical forests release substantial quantities of biogenic volatile organic compounds (VOCs) to the atmosphere (Guenther et al. 1995). VOC release is important to the ecosystem carbon balance (Crutzen et al. 1999; Kesselmeier et al. 2002a). A full accounting of the influence of VOCs on ecosystem carbon budgets must consider both sources and sinks for these compounds and the reaction products of VOCs including atmospheric particulates. One of the key issues here is the large biodiversity of Amazonia, because VOC emissions (such as isoprene and  $\alpha$ -pinene emissions) are specie-dependent (Guenther et al. 1995). Greenberg et al. (2004) and Harley et al. (2004) employed tethered balloon and leaf measurements approach to study the distribution of VOCs in Amazonia. Similar to the threefold variation that Malhi et al. (2004) reported for woody biomass production across the basin, these authors found a threefold variation in emission rates of VOCs across different regions, and they attributed this variation to diverse species composition. Also significant seasonal variability is found, with Kuhn et al. (2002, 2004) reporting up to a twofold difference in isoprene emissions between wet and dry seasons in Rondônia. Due to diversity of environments and species richness, we can expect to find similar variability in other regions in Amazonia.

Canopy emissions of VOCs amount to a few percent of net primary productivity (Guenther 2002; Kesselmeier et al. 2002a; Wiedinmyer et al. 2004), but their effects on atmospheric chemical processes and physical climate processes far exceed their modest contribution to the C cycle. Recently, Clayes et al. (2004) showed that isoprene emissions in Amazonia could make up a significant fraction of cloud condensation nuclei and thus have a role in precipitation patterns. Biogenic hydrocarbons are critically important in the regulation of concentrations of ozone, hydroxyl radical and other important trace gases and radicals in tropical atmospheric chemistry (Andreae et al. 2001). Terpenes are precursors of radiation forcing aerosol particles, which also act as cloud condensation nuclei, but terpene concentrations amount to only a few parts per billion in several sites in Amazonia (Kesselmeier et al. 2002b). Still, part of the precipitation formation mechanism could be controlled by the vegetation itself through isoprene and terpene emissions (Artaxo et al. 2002; Clayes et al. 2004). Hence, links between the biosphere and the atmosphere appear to be extremely complex, with climate affecting VOC emissions and vice versa in a highly non linear process

(Kesselmeier et al. 2000, 2002a, b; Wiedinmyer et al. 2004).

---

## Measurements of carbon exchange at the ecosystem level

### Eddy covariance studies

The accurate measurement of trace gas exchange at the Earth's surface is important in order to evaluate ecosystem functioning and to show environmental and process changes such as CO<sub>2</sub> fluxes, climate fluctuation, atmospheric chemistry, or nutrient cycling. Among several techniques the eddy correlation, or eddy covariance, is one of the most direct and useful. Eddy correlation can be used to validate surface vegetation-atmosphere transfer schemes, and thus improve climate and ecosystem predictability. The exchange rate of CO<sub>2</sub> across the interface between the atmosphere and a forest canopy is determined through measuring the covariance between fluctuations in vertical wind velocity and CO<sub>2</sub> mixing ratio (Baldocchi 2001, 2003). These exchanges measured by flux towers have taught a few remarkable lessons:

- Atmospheric CO<sub>2</sub> fluxes showed seasonal variability, linked to basin scale spatial variability of climate and local scale biogeochemistry.
- Surface energy partition and evapotranspiration are often tied to the CO<sub>2</sub> flux variability.
- Structural differences between the tropical forests and Cerrado (savanna) physiognomies, or pasturelands, were corroborated by measured fluxes.
- Wetlands function substantially different from dry lands. Wetland contribution might be related to the carbon budget of the entire basin, and dependent on the flood-pulse variability.
- Site-specific characteristics (e.g. geomorphology, past disturbances) constrain the measured CO<sub>2</sub> flux variability.
- The combination of annual accumulation of CO<sub>2</sub> fluxes with biometric measurements can help infer the sink or source role of a plant community, regardless of its transient daily character.

Although eddy covariance technique has provided reliable measurements of bulk photosynthesis and respiration of temperate forest sites (Baldocchi et al. 1997; Jarvis et al. 1997), there are situations where its capacity to provide accurate integrated measurements of net carbon exchange is uncertain. The uncertainties stemmed from difficulties related to (1) night time fluxes, when respired CO<sub>2</sub> tend to accumulate within the forest canopy and intermittent updraft events transfer it to the atmosphere in a complex spatial pattern not consistently caught by the flux tower sensors (Staebler and Fitzjarrald 2004), and (2) an irregular topography, where lateral CO<sub>2</sub> advection to lower positions on the landscape, can result in CO<sub>2</sub> draining out from the eddy covariance tower footprint (Araujo et al. 2002).

Since last decade, the continuous use of eddy covariance technique and microclimate measurements has amassed an impressive body of information on the CO<sub>2</sub> and water vapor cycle within Amazonian boundaries (Fig. 3). Variability in seasonal CO<sub>2</sub> flux of *terra firme* forests was noticed among sites of eastern (Caxiuanã, Tapajós), central (Cuieiras) and southern (Jarú) regions of the Amazon basin. At Tapajós and Caxiuanã, there was no evidence of drought stress during the dry season as evapotranspiration peaked concurrently with decreasing cloud cover and increasing surface net radiation (Carswell et al. 2002; Rocha et al. 2004). Minimum NEE peaked before the wet season (nearly October) at the eastern sites, where carbon was taken up in the dry season and released in the wet season, based on 3 years of observation (2000–2003) (Saleska et al. 2003; Carswell et al. 2002; Goulden et al. 2004). This pattern was explained by an increase in soil respiration (and wood biomass) in the wet season, and a substantial reduction in the dry season, while gross ecosystem productivity (GEP) responded weakly on a seasonal basis. GEP was lowest in July, when the incoming solar radiation is also lowest. The net carbon uptake peak late in the dry season and the minimum GEP are partly explained by the flushing of new leaves and the innate seasonal rhythms of the vegetation (Goulden et al. 2004). Events like the reduction of precipitation due to ENSO warm episodes, can cause a reduction in net primary productivity (NPP) as evidences shown by Townsend et al. (2002), enhancing the seasonality on CO<sub>2</sub> fluxes in Amazonia.

Among the sites previously mentioned, at Cuieiras the average NEE shows a weak seasonal variability, suggesting a lower average carbon uptake in the dry season ( $-17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) relative to the wet season ( $-21 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) (Malhi et al. 1998; Araujo et al. 2002). As opposed to Tapajós, at Cuieiras, there appeared to be limited reduction of soil respiration in the dry season. This could be related to the shorter dry season length in the Manaus region ( $\sim$  July–October) than in Tapajós ( $\sim$  July–December). Given that, observations at Cuieiras were taken partly over poorly drained valleys (contrasting to the observations over flatter and well-drained plateaus at Tapajós), where soils saturate more often (Chambers et al. 2004), a shortest dry season could prevent large moisture depletion (Davidson et al. 2000). This combined with small but significant increases in air and soil temperatures, could prevent a large soil respiration reduction. Possibly also related to different dry season lengths, the seasonal amplitude of NEE appeared larger in Tapajós ( $\sim 700 \text{ kg C ha}^{-1} \text{ month}^{-1}$ ) than in Cuieiras ( $\sim 150 \text{ kg C ha}^{-1} \text{ month}^{-1}$ ) (Saleska et al. 2003; Araujo et al. 2002).

At Jarú site, net carbon uptake is reduced continuously throughout the dry season (June–August), as opposed to Tapajós, and with larger seasonal amplitude than Cuieiras (Kruijt et al. 2004; von Randow et al. 2001). This pattern, observed at Jarú transitional tropical forest, is influenced by recurrent cooler temperatures

( $\sim 13^\circ\text{C}$ ) in the winter, and responds similarly to semi-deciduous forests, where leaf senescence is pronounced in the dry season. Culf et al. (1996) reports increasing solar albedo during May–August at the Jarú site, concurrent with soil moisture depletion, which partly explains the changes in phenology and the CO<sub>2</sub> fluxes. The authors observed a similar variation in albedo in the Manaus region (Reserva Ducke forest), although seasonality in CO<sub>2</sub> fluxes was less evident in Cuieiras so far.

Over the Cerrado sites (savannas to the South), a net carbon uptake clearly occurs during the wet season, whereas strong positive NEE occurs in the late dry season. This pattern is markedly shown in the transitional mature forest (Cerradão) ( $11.5^\circ\text{S}$ ) (Vourlitis et al. 2001) and over a Cerrado restrito site in Brasilia ( $16^\circ\text{S}$ ) (Miranda et al. 1996). Vourlitis et al. (2004) stress the remarkable reduction in evapotranspiration during the dry season over Cerradão. Vourlitis et al. (2001) showed that the NEE of Cerradão was similar to that of tropical rainforest during the wet season (a net sink between  $-0.6 \mu\text{mol}$  and  $-1.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , during February and April), but during the dry season it was more similar to that reported for tropical savanna, being in balance during August–September, and a net source of  $0.6 \mu\text{mol}$  and  $1.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  during October–November. A comparable variability was observed over a Cerrado restrito site down in southeast Brazil ( $18^\circ\text{S}$ ) (Rocha et al. 2002). This is very suggestive that despite the latitudinal and climate differences among sites, adaptive mechanisms of these species can exert a large and common control on the carbon exchanges for the Cerrado biome.

Over dry forests, plant gross primary productivity (GPP) increases during the wet season, as seasonal drought results in a negative water balance in the trees and a reduction in stem growth. In seasonally flooded forests, however, tree growth occurs during the terrestrial (dry) phase (Dezzeo et al. 2003; Schongart et al. 2002), as flooding causes leaf shedding. It is predicted that GPP starts to increase at the end of the aquatic phase, when the leaves flush. Interannual variability also increases plant GPP, in these forests, as a reduction in precipitation by ENSO warm episodes in eastern and central Amazonia reduce the period of inundation (Schongart et al. 2004). Atmospheric NEE observations in the Bananal Island (characterized by a seasonally flooded ecotone Cerradão-Cerrado-campo) show a reduction in ecosystem nocturnal respiration during the aquatic phase (February–April) and consequently increasing ecosystem carbon uptake (H. Rocha in preparation).

Conversion of tropical forests to pasturelands in Amazonia reduces evapotranspiration, mostly in the dry season (Wright et al. 1992), and the moisture status in the root zone (Hodnett et al. 1995). The control of carbon exchanges become variable and largely dependent of the crop physiology and management. Sakai et al. (2004) measured the turbulent CO<sub>2</sub> fluxes over agricultural fields in Santarém, in a succession of pas-



ture, plowed bare soil and a rice plantation. They observed a larger average carbon uptake over the rice plantation (non-irrigated) ( $-7.0 \pm 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) compared to the pasture ( $-2.3 \pm 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the wet season and  $-1.6 \pm 0.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the dry season). Plowed bare soil in between these two plantations showed an average loss of  $1.8 \pm 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .

While it seems unlikely that as large a carbon uptake as  $6 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  reflects a steady ecosystem state (Chambers et al. 2001b), it is also not obvious that the sum of instantaneous  $\text{CO}_2$  fluxes always provides a realistic estimate of average net ecosystem production. Lack of air turbulence and insufficient mixing of  $\text{CO}_2$  from canopy respiration during the night often is corrected with the measurement of a storage term. These corrected fluxes are intended to achieve better accuracy in estimating the amplitude of diurnal and seasonal cycles and the variability among sites in Amazonia.

However, the generally presumed conditions of flat and drainage-free surfaces along the tower fetch are rarely found. Thus, local topography and air-mass circulation are crucial (Araujo et al. 2002). Accounting for these site-specific problems is not trivial (Staebler and Fitzjarrald 2004). The hypothesis that low turbulence during nighttime is correlated proportionally to drainage losses, suggests that the use of thresholds based on turbulence scales (such as  $u^*$  used in deciduous forests; Goulden et al. 1996) may be effective for some sites in Amazonia. This would allow the replacement of nighttime low-turbulent events with well-mixed ones (Miller et al. 2004; Araujo et al. 2002; Saleska et al. 2003). This may improve the realism of the NEE annual sum (Saleska et al. 2003). However, the accurate application of turbulence filters to a given site's data requires parameters from other studies, such as using radon as proxy for  $\text{CO}_2$  transport within the canopy (Martens et al. 2004) or from direct measurement of in-canopy advection (Staebler and Fitzjarrald 2004). Until the problem of topography-related  $\text{CO}_2$  loss is properly resolved, with the development of widely accepted eddy-flux correction methodology, site-dependent estimates of NEE annual sums for Amazonian forests remain uncertain.

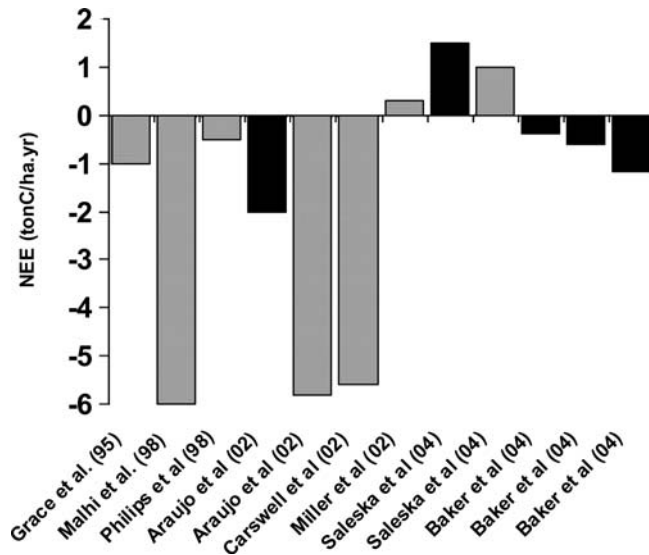
---

## Biometry studies

The annual allocation of photosynthetic products to wood growth is estimated from the annual biomass increment in a forest stand. This is achieved either through repeated surveys of trees (Baker et al. 2004a, b) or through the use of dendrometer bands assigned to representative trees within the stand (Rice et al. 2004; Vieira et al. 2004). Such forest inventory plots were used to infer average net storage in live biomass of undisturbed tropical forests. However, these measurements only account for inter-annual and stand level variations over a relatively short time scales and limited spatial

coverage. The evaluation of residence time for carbon in vegetation is critical for carbon storage calculations, thus growth rates, stand and vegetation ages are essential measurements for carbon dynamic studies. Houghton et al. (2000) observed that the previous biomass of deforested areas was the major uncertainty in the estimation of carbon flux to the atmosphere. The uncertainties in biomass estimates have several causes. Maybe one of the most important and difficult to solve is the natural heterogeneity of tropical forests. According to Thomaz (2000) there may be up to 35,000 species of angiosperms in the Amazon basin. But the extent of the potential diversity still to be found is unknown (Tuomisto et al. 1995), and may render this last estimate a conservative one. Still, this number represents almost 14% of all known angiosperms species in the globe, encompassed in an area equivalent to 4.7% of the land area on Earth. While on one hand, such high biodiversity is a joy of life, on the other hand, it makes allometric biomass measurement a logistical nightmare. As there are hundreds of different individuals and species per hectare, it is expected high variability on form, height, wood density and structure within a site (Clark 2004). Besides this in-site variability there is also important variability among different regions due to differences in soil composition and climatic differences (Malhi et al. 1999; Marengo and Nobre 2001).

Thus, the mega complexity of this ecosystem engendered several questions related to above ground biomass estimation (Keller et al. 2001; Brown et al. 1995). The most common methods to tackle these questions are: (1) direct estimates by cutting and weighting all trees above 10 cm diameter at breast height (DBH) over a relatively small area, generally smaller than 0.5 ha (Phillips et al. 2004) or (2) indirect estimates by using allometric equations (Chambers 2001; Gerwing and Farias 2000; Brown et al. 1995). These equations are obtained by cutting and weighting a determined number of trees and relating their biomass with DBH and height. Estimates of biomass in Amazonia may involve scattered measurements of DBH and height over large areas, like the measurements made by the RADAMBRASIL project or over small areas (generally smaller than 5 ha) (Houghton et al. 2001). Although it seems simple, measurement of parameters like DBH can be difficult in tropical forests, resulting in large errors in biomass estimation (Clark 2002). In addition, it seems that the choice of the right allometric equation is of fundamental importance to reduce those errors (Chave et al. 2004). Most of the live biomass, growth, mortality and recruitment measurements are taken on permanent forest transects, located in more representative parts of the studied forest. Normally, longer transects aims to incorporate spatial heterogeneity avoiding bias associated with small-scattered plots that can be disproportionately influenced by emergent trees (Rice et al. 2004). Brown et al. (1995) support the general idea that in tropical forests, the aboveground biomass is dominated by few large trees, showing as example a forest in western Amazonia where



**Fig. 6** Estimates of net ecosystem exchange (NEE) obtained by eddy covariance technique (*open bars*) and by aboveground biomass estimates (*black bars*). NEE values are plotted according to the year of publication. Grace et al. (1995a)—eddy covariance technique, Ji-Paraná; Malhi et al. (1998)—eddy covariance technique, Manaus; Phillips et al. (1998)—biomass inventory, several sites; Araujo et al. (2002)—eddy covariance technique Manaus; Carswell et al. (2002)—Reserva Caixuanã; Miller et al. (in press)—biomass inventory, Santarém; Saleska et al. (2003)—biomass inventory, Santarém; Saleska et al. (2003)—eddy covariance technique; Baker et al. (2004)—biomass inventory, eastern and central plots, western plots and floodplain plots, respectively

trees with DBH above 60 cm account for 50% of the biomass. In this transect, trees are identified and dendrometers are placed in a random sub-sample within the plot, but distributed across taxonomic families and sizes. The dendrometers normally used are stainless-steel bands (Rice et al. 2004; Vieira et al. 2004) or automated systems (Miranda 2002; Silva et al. 2002). Baker et al. (2004a, b) produced three estimates based on aboveground measurements in plots. Their results were clustered in three groups: east and central plots; western plots and floodplain plots. The east and central plots showed the smallest carbon gain ( $-0.37 \text{ ton C ha}^{-1} \text{ year}^{-1}$ ) and the floodplain forest plots the largest carbon gain ( $-1.2 \text{ ton C ha}^{-1} \text{ year}^{-1}$ ).

In recent study, Vieira et al. (2004) has illustrated a high diversity among three study plots located in terra-firme forests near Manaus, Rio Branco and Santarém (Table 1). The range in number of species per hectare in these plots was similar to that in other 16 other plots summarized by Oliveira and Nelson (2001) that show a range from 90 up to 285 species per hectare in Amazonian terra-firme forests.

An important aspect of aboveground biomass, especially wood, is the residence time of carbon in this pool. This is related to functional group, forest stand, nutrient availability and environmental conditions. Condit et al. (1995) have shown large increases in tree mortality associated with extremely dry conditions in tropical forests. The difference in adaptation to extreme condi-

**Table 1** Number of individuals with diameter at breast height higher than 10 cm/ha followed by the number of botanical families and species in Manaus, Rio Branco and Santarém (Vieira et al. 2004)

	Manaus	Rio Branco	Santarém
Individuals	626	466	450
Family	52	40	50
Species	232	164	265

tions potentially leads to changes in how biomass is distributed among different functional types (Philips and Gentry 1994). Also, the accumulation of C in living wood may be offset by tree mortality; hence the degree to which a forest is acting as a source or sink of C to the atmosphere is not solely dependent on the growth rate of living wood. Understanding mortality, its spatial and temporal distribution, and its relationship to climate and disturbance (such as fire, for instance) are critical points to be considered when attributing mean life time for trees on global models of climatic change. Chambers et al. (1998) found that the ages of emergent trees (DBH varying from 80 cm to 240 cm) sampled near Manaus, central Amazonia, varied from 200 years to 1,400 years, although such millenary trees were not documented by other investigations anywhere else in the tropics (Worbes 2002).

Besides the high variability in tree age reported for a single site, radiocarbon ages determined in several trees in Manaus, Rio Branco and Santarém showed also a large within site variability, as well as a high variability among sites (Vieira et al. 2004). For instance, the mean radiocarbon age in Manaus was 306 years, while in Santarém the mean radiocarbon age was much younger, approximately 160 years (Simone Vieira and Plínio Camargo, personal communication). Overall, the few results shown so far indicate that mean tree age in Amazonia appears to be higher than 42 years as used in some models.

## NEE of Amazonia

Several papers based on modeling terrestrial NPP (Friedlingstein et al. 1995; Mellilo et al. 1996; Thompson et al. 1996; McGuire et al. 1997) have shown that tropical forests could be one of the key biomes in the modern global carbon cycle. Nevertheless, the first estimate of tropical NEE produced by atmospheric inverse model calculations showed a high degree of variability, revealing no  $\text{CO}_2$  emission pulse created by tropical deforestation (Schimel et al. 2001). This was taken as indirect evidence that the tropics could be acting as an important carbon sink, as deforestation was widespread in this region. Several basin-wide estimates, proposed since the beginning of the 1990s for Amazonia, are summarized in Fig. 6. The first local measurement made by Grace et al. (1995a), using eddy covariance technique,

found a net carbon gain of approximately  $1 \text{ ton C ha}^{-1} \text{ year}^{-1}$ . This net gain led to a lively debate about the role of the Amazonia forests as an important sink for carbon. Few years later, a second similar eddy covariance study, comprised of an entire year of observations in central Amazonia, found a net carbon gain almost sixfold larger than that of the first study (Malhi et al. 1998). Tropical forests are one of the largest carbon reservoirs among terrestrial systems (Field et al. 1998), thus changes of this magnitude in these ecosystems would affect planetary scale processes. In the same year, the first large compilation of stand biomass growth data in several tropical sites corroborated the eddy covariance findings of net gain, but pointed to a sink magnitude closer to the figure of the first eddy covariance study (Phillips et al. 1998). The idea that primary forests could be large sinks of C directly challenged the ecological assumption of mature forests as being in “a long term climax”. Grace and colleagues attributed this uptake to a  $\text{CO}_2$  fertilization effect. A series of measurements have tested the  $\text{CO}_2$  fertilization claim (see Fig. 6 and item 4.1) (Laurance et al. 2004; Phillips et al. 2002a; Johnson et al. 2001; Lloyd et al. 2001; Malhi et al. 1999; Nelson et al. 1999), but to our knowledge no research result has yet demonstrated a clear causal relationship between Amazonian rainforest growth and an increased atmospheric  $\text{CO}_2$  concentration.

As most of the early estimates of NEE pointed towards a carbon gain by the forest, several studies attempted to locate the potential extra carbon storage in the Amazonian ecosystems. Some claimed upfront that very large uptake by these forests was ecologically unrealistic (Keller et al. 2001), mainly because there would be nowhere to store the implied large amount of carbon. Malhi and Grace (2000) considered the hypothesis that the majority of the extra carbon was accumulating in the soil organic matter at a rate of  $3.5 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ . However, Telles et al. (2003) have estimated carbon stocks from 102 Mg to 151  $\text{Mg C ha}^{-1} \text{ year}^{-1}$  with storage rates of  $0.09\text{--}0.13 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  (they considered a  $0.5\% \text{ year}^{-1}$  increase in ecosystem productivity), and with additional potential storage of  $0.18\text{--}0.27 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  in surface litter and roots. These authors have reported turnover rates in the soil organic matter pool of less than 10 years; however, for the last 20 years, a stable carbon stock was identified in primary forests of the Manaus region, suggesting a low possibility of these soils being potential carbon sinks for the considered period (Telles et al. 2003). Residence time and fluxes of carbon in or out of the soil and the time of residence of this carbon in the soil profile are key factors in estimating the importance of this compartment to the carbon balance in a forest system. Studies by Camargo et al. (1999) and Bernoux et al. (2002) have shown that the majority of carbon stocks in the soil are associated with recalcitrant compounds (coal, lignin, etc.) that do not turnover on the timescales of decades or centuries. Thus, production

and decomposition of wood predominates the dynamic carbon stock of these forests (Chambers et al. 2000; Phillips et al. 1998). Recent data from three sites in Amazonia (Chambers et al. 2004; Viera et al. 2004; Silva et al. 2002) have shown that tree growth and mortality rates are too slow to account for the amount of carbon similar to that indicated by early eddy covariance studies. Chambers et al. (2004) using stochastic-empirical modeling of carbon dynamics of live and dead trees for one site central Amazonia indicated that the forest can support only a 0.5% increase in NPP over a long period. However, these authors warn that their “...predictions about whether or not old-growth tropical forests will act as carbon sources, sinks, or remain in overall balance, depends on assumptions for which reliable field data are often not available.” (Chambers et al. 2004).

The site-specific question was addressed in a recent work by Saleska et al. (2003). The authors presented eddyflux NEE estimates at Tapajós, with biometric measurements suggesting that the site was under the effects of transient disturbance. These could include recent past ENSO warm episodes, which may have caused anomalously large mortality rates and have potentially offset carbon uptake during the recovery. Keller et al. (1996) have shown that the fall of a giant emergent tree can result in a loss of about  $750 \text{ kg C ha}^{-1}$  over 13 ha within a few years. These authors also pointed out that recovery from long-term climate stress could otherwise lead to net carbon uptake in the present. These uncertainties suggest that there is a large spatial variability over terra firme tropical forests in Amazonia, and that average annual NEE estimates should combine biometric measurements with climate interannual variability to provide more accurate assessments.

The aquatic systems are another important component of the Amazonian ecosystem that need to be considered for a regional carbon balance. Richey et al. (2002) estimated that up to  $1.2 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  could be lost to the atmosphere in a large swath of central Amazonia. Extrapolation across the entire flooded area of the basin produced an emission of approximately  $0.5 \text{ Pg C year}^{-1}$ , which is of the same magnitude as the carbon emission caused by land-use changes in Tropical Latin America (DeFries et al. 2002). Contrastingly, Waterloo et al. (in preparation) have recently concluded, from a continuous long-term measurement in a monitored black water catchment near Manaus, that typical terra-firme forest export a significantly smaller load of dissolved organic compounds ( $< 0.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ) than speculated by Richey et al. (2002). This transfers the potential source of the estimated riverine emissions to productive ecosystems within whitewater floodplains (Junk 1997; Piedade et al. 2000). Shedding a little more light on this controversy, eddyflux measurements were carried out for a complete seasonal cycle in the Pantanal wetland area, near the border of Brazil and Bolivia, to the South of Amazonia (Manzi et al. 2002). These measurements have indicated a marked source during the flood period, similar to the estimate of Richey et al.

(2002), but have also shown a strong sink in the ebb season (Manzi et al. 2002). The reversal in carbon balance is probably due to vigorous revegetation by C4 grasses and other floodplain plants (Piedade et al. 2000), confirming the potential importance of productivity within the floodplain in balancing the total exchange of these biomes with the atmosphere. In addition, radio-carbon measurements (Emilio Mayorga and Anthony Aufdenkampe, personal communication) show that most emitted C is relatively recent in origin—aquatic systems lose C to the atmosphere rapidly enough so that adjustments to change would be instantaneous. Therefore, the role of aquatic systems in local to regional C budgets will depend primarily on the temporal balance of CO<sub>2</sub> sources in the flood season and CO<sub>2</sub> sinks in the ebb season. However, the origin of the CO<sub>2</sub> being lost to the atmosphere (e.g. in-stream or riparian processes vs. export from uplands) and how long it takes for C to transit to the aquatic system (without significant—e.g. decadal—time lags, there can be no net storage or loss) also need to be considered. The importance of aquatic systems will also depend on their potential for change with land use or climate, a matter still under investigation.

More recently, a series of articles called for caution in interpreting potential gains of carbon by biomass in the Amazonia (Chambers and Silver 2004; Clark 2004; Körner 2004). In short, the main message of these studies may be summarized by two sentences from Christian Körner works: (1) “a stimulation of assimilation does not necessarily mean that there is more growth”, and (2) “a stimulation of growth does not necessarily mean enhanced carbon sequestration”. Thus the C storage under a NEE perspective is also dependent on changes in the dynamic structure, or regrowth, of forests. A change from emergent trees to lianas and small trees (Laurance et al. 1997; Phillips et al. 2002b) can reflect a net carbon loss to the atmosphere. Another key issue, illustrated by LBA project, is that the Amazonian ecosystems have very large capacity for interannual shifts in C balance (i.e. the interannual variation in the wood storage term shown by Vieira et al. 2004).

In order to place Amazonia in a global perspective and make the carbon flux obtained through the LBA project comparable with global carbon budgets, we extrapolated NPP/NEE values found by (several) LBA studies to the entire area of Brazilian Amazonia covered by rainforest. We are fully aware of the tremendous variability across ecosystems of Amazonia, and this heterogeneity could make invalidate our simple extrapolation. Nevertheless we feel it is important to make a first approximation, such as this, in order to compare the carbon flux measured in the Amazonia plots with global carbon estimates (Fig. 7).

An recent comparison of atmospheric CO<sub>2</sub> inversion models indicated that tropical lands in the Americas could be a net source of  $0.62 \pm 1.15 \text{ Pg C year}^{-1}$  (Gurney et al. 2002). This

contrasts with estimates by Schimel et al. (2001) where the tropics appear as a neutral source or sink for carbon. Both, Gurney et al. (2002) and Schimel et al. (2001), stressed that uncertainties in the tropical regions of the world are much greater than elsewhere due to the lack of an adequate and accurate CO<sub>2</sub> concentration measurement network.

The four last estimates of carbon flux in the tropics due to land use changes produced different values. Fearnside (2000) and Houghton (2003) using deforestation rates from FAO estimated  $2.4 \text{ Pg}$  and  $2.2 \text{ Pg C year}^{-1}$ , respectively, for the net flux due to land use changes in the tropics. Achard et al. (2002) and DeFries et al. (2002), based on deforestation inferred directly from satellite data, produced lower estimates for the tropics of  $0.96 \text{ Pg C year}^{-1}$ , respectively. If the estimates of Fearnside (2000) and Houghton (2003) of tropical deforestation are correct, the emission term in the tropics would be approximately  $2.3 \text{ Pg C year}^{-1}$ . However, the inversion models are capturing in average total emissions of only  $0.62 \text{ Pg C year}^{-1}$ . Forgetting for a moment the uncertainty of the inversion models, this would imply that there must be a local sink of approximately  $1.6\text{--}1.7 \text{ Pg C year}^{-1}$ , which would be equivalent to a net gain of  $2.7 \text{ ton C ha}^{-1} \text{ year}^{-1}$  in areas of pristine rainforest. If the estimates by Achard et al. (2002) and DeFries et al. (2002) are correct, conversion of tropical forests would be releasing to the atmosphere an average of  $0.93 \text{ Pg C year}^{-1}$ . In this scenario, a smaller C sink of approximately  $0.31 \text{ Pg C year}^{-1}$  would be needed then to satisfy the inversion models, resulting in a potential sink strength for pristine forests of  $0.85 \text{ ton C ha}^{-1} \text{ year}^{-1}$ . In this case, the tropical forests would act as source of carbon to the atmosphere equivalent to  $0.85 \text{ ton C ha}^{-1} \text{ year}^{-1}$ . Using our crude extrapolation of LBA values for the Amazon forests ( $5 \text{ million km}^2$ ) we come out with a carbon exchange estimate varying from  $-3.0 \text{ Pg}$  to  $0.75 \text{ Pg C year}^{-1}$  (Fig. 7).

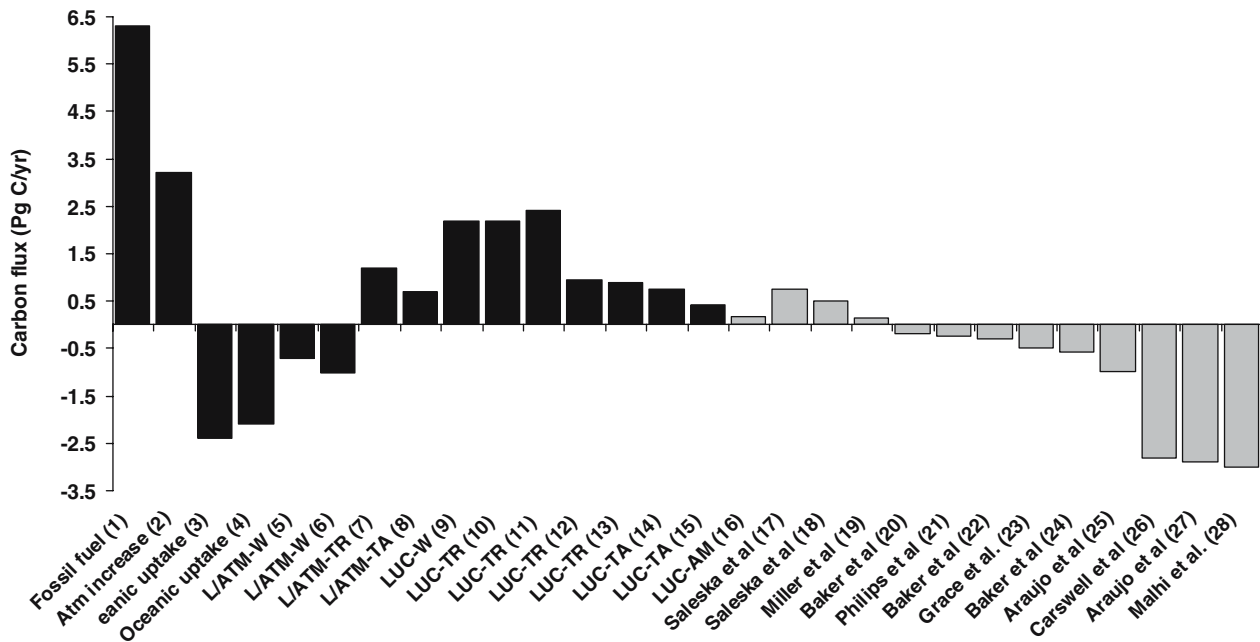
---

## Conclusions

There is a large uncertainty in carbon fluxes estimates for the tropics as a whole and in Amazonia in particular bring the awareness that we have not enough information to decide whether Amazonia is a carbon source or sink, or if it is both, depending on climatic variation and the rates of forest conversion. The accumulation of sufficient information for a huge system such as the Amazon region has to advance step by step.

The future of the carbon balance, especially in the Brazilian Amazonia, is closely related to the economy. As the Brazilian economy grows, deforestation rates may increase if the government does not provide environmentally sustainable regulation. Increasing deforestation rates might overwhelm a potential sink by primary and regrowth forests.





**Fig. 7** Carbon flux from several sources. Positive numbers denote sources of carbon to the atmosphere and negative numbers denote an uptake of carbon from the atmosphere. *L/ATM* denotes a flux from the land to the atmosphere; *LUC* denotes a flux due to land use changes. *W* World; *TR* Tropics; *TA* Tropical America; and *AM* Amazonia. (1) Fossil fuel emissions (Schimel et al. 2001); (2) Atmosphere increase in CO<sub>2</sub> (Schimel et al. 2001); (3) Estimate of ocean uptake of CO<sub>2</sub> (House et al. 2003); (4) Estimate of ocean uptake of CO<sub>2</sub> (Houghton 2003); (5) Estimate of terrestrial sink of carbon (Houghton 2003); (6) Estimate of terrestrial sink of carbon (House et al. 2003); (7) Source of carbon from total tropical lands to the atmosphere estimated by inversion models (Gurney et al. 2002); (8) Source of carbon from tropical lands of the Americas to the atmosphere estimated by inversion models (Gurney et al. 2002); (9) Source of carbon from lands of the entire world to the atmosphere due to land use changes (Houghton 2003); (10) Source of carbon from tropical lands to the atmosphere due to land use changes (Houghton 2003); (11) Source of carbon from tropical lands to the atmosphere due to land use changes (Fearnside 2000); (12) Source of carbon from tropical lands to the atmosphere due to land use changes (Achard et al. 2002); (13) Source of carbon from

The complex sink/source duality of Amazonia was discussed extensively in the literature and during several scientific meetings of the LBA project; however, no strong conclusions were drawn, other than the ones presented in this work. The valuable data emerging from the pioneering network of flux towers and forest plots in Amazonia bring, for the first time, the unique chance to compare and understand diverse and contrasting ecophysiological processes. Process models have yet to capture this immense complexity in a fine resolution. Certainly, it is an important and vital question for Brazil and for the world from many perspectives. However, by paying too much attention to the issue of uniqueness of a sink or source character and finding its magnitude, we may lose a great opportunity to discuss the basic functioning and the complexities of the ecosystems in Amazonia.

**Acknowledgements** Jean Pierre H.B.Ometto, Luiz Martinelli and Humberto Rocha acknowledge FAPESP and NASA, through

tropical lands to the atmosphere due to land use changes (DeFries et al. 2002); (14) Source of carbon from tropical lands of Americas to the atmosphere due to land use changes (Houghton 2003); (15) Source of carbon from tropical lands of Americas to the atmosphere due to land use changes (DeFries et al. 2002); (16) Source of carbon from tropical lands of the Amazonia basin to the atmosphere due to land use changes (Houghton et al. 2002). Estimates from number 17–28 are carbon flux estimates made by several groups of the LBA project. Originally these fluxes were presented as tons of C per hectare. We extrapolated them to an area of 5 million km<sup>2</sup> of forest (see text for details). (17) Saleska et al. (2003)—biomass inventory; (18) Saleska et al. (2003)—eddy covariance technique; (19) Miller et al. (in press)—biomass inventory; (20) Baker et al. (2004)—biomass inventory; (21) Phillips et al. (1998)—biomass inventory; (22) Baker et al. (2004)—biomass inventory; (23) Grace et al. (1995)—eddy covariance technique; (24) Baker et al. (2004)—biomass inventory; (25) Araujo et al. (2002)—eddy covariance technique; (26) Carswell et al. (2002)—eddy covariance technique; (27) Araujo et al. (2002)—eddy covariance technique; (28) Malhi et al. (1998)—eddy covariance technique

LBA, for financial support. Antonio D. Nobre acknowledges support from PPG7-FINEP, European Commission and CNPq. Paulo Artaxo acknowledges the Millennium Institute from CNPq and FAPESP for financial support. The authors acknowledge Adam West, Suzan Trumbore and an anonymous reviewer for great and critical contribution that improved the accuracy and clarity of this paper.

## References

- Achard F, Eva HD, Stibig HJ, Mayaux P, Galleo J, Richards T, Malingreau JP (2002) Determination of deforestation rates of the world's humid tropical forests. *Science* 297:999–1002
- Andersen LE, Granger CWJ, Reis EJ, Weinhold D, Wunder S (2002) The dynamic of deforestation and economic growth in Brazilian Amazonia. Cambridge University Press, UK
- Andreae MO, Artaxo P, Fischer H, Freitas SR, Gregoire JM, Hansel A, Hoor P, Kormann R, Krejci R, Lange L, Lelieveld J, Lindinger W, Longo K, Peters W, de Reus M, Scheeren B, Dias MAFS, Strom J, van Velthoven PFJ, Williams J (2001)

- Transport of biomass burning smoke to the upper troposphere by deep convection in the equatorial region. *Geophys Res Lett* 28(6):951–954
- Andreae MO, Almeida SS, Artaxo P, Brandão C, Carswell FE, Ciccioli P, Culf A, Esteves JL, Gash J, Grace J, Kabat P, Lelieveld J, Malhi Y, Manzi AO, Meixner FX, Nobre AD, Nobre C, Lourdes Ruivo MA, Silva-Dias MA, Stefani P, Valentini R, von Jouanne J, Waterloo M (2002) Biogeochemical cycling of carbon, water, energy, trace gases and aerosols in Amazonia: the LBA-EUSTACH experiments. *J Geophys Res* 107(D20):8066–8091. DOI 10.1029/2001JD000524
- Andreae MO, Rosenfeld D, Artaxo P, Costa AA, Frank GP, Longo KM, Silva-Dias MAF (2004) Smoking rain clouds over the Amazon. *Science* 303(5662):1337–1342
- Araujo AC, Nobre AD, Kruijt B, Culf AD, Stefani P, Elbers J, Dallarosa R, Randow C, Manzi AO, Valentini R, Gash JHC, Kabat P (2002) Dual tower longterm study of carbon dioxide fluxes for a central Amazonian rain forest: the Manaus LBA site. *J Geophys Res Atmos* 107(D20):8090. DOI 10.1029/2001JD000676
- Artaxo P, Martins JV, Yamasoe MA, Procopio AS, Pauliquevis TM, Andreae MO, Guyon P, Gatti LV, Leal AMC (2002) Physical and chemical properties of aerosols in the wet and dry seasons in Rondonia, Amazonia. *J Geophys Res Atmos* 107(D20):8081
- Avissar R, Silva Dias PL, Silva Dias MAF, Nobre C (2002) The large-scale biosphere-atmosphere experiment in Amazonia (LBA): insights and future research needs. *J Geophys Res Special LBA Issue* 107. DOI 10.1029/2002JD002704
- Baidya Roy S, Avissar R (2002) Impact of land use/land cover change on regional hydrometeorology in Amazonia. *J Geophys Res* 107(D20). DOI 10.1029/2000JD000266
- Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Killen T, Laurance SG, Laurance WL, Lewis SL, Lloyd J, Monteagudo A, Neill DA, Patino S, Pitman NCA, Silva N, Vasquez MR (2004a) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biol* 10(5):545–562
- Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Monteagudo A, Neill DA, Vargas PN, Pitman NCA, Silva JNM, Martinez RV (2004b) Increasing biomass in Amazonian forest plots. *Phil Trans R Soc Lond B*. DOI 10.1098/rstb.2003.1422
- Baldocchi DD, Vogel CA, Hall B (1997) Seasonal variation of energy and water vapor exchange rates above and below a boreal jack pine forest canopy. *J Geophys Res Atmos* 102(D24):28939–28951
- Baldocchi D, Finnigan J, Wilson K, Paw KT (2000) On measuring net ecosystem carbon exchange over tall vegetation in complex terrain. *Bound Layer Meteorol* 96:257–291
- Baldocchi D, Falge E, Gu LH, Olson R, Hollinger D, Running S, Anthoni P, Bernhofer C, Davis K, Evans R, Fuentes J, Goldstein A, Katul G, Law B, Lee XH, Malhi Y, Meyers T, Munger W, Oechel W, U KTP, Pilegaard K, Schmid HP, Valentini R, Verma S, Vesala T, Wilson K, Wofsy S (2001) FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bull Am Meteorol Soc* 82:2415–2434
- Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biol* 9(4):479–492
- Bernoux M, Carvalho MDS, Volkoff B, Cerri CC (2002) Brazil's soil carbon stocks. *Soil Sci Soc Am J* 66(3):888–896
- Bousquet P, Peylin P, Ciais P, Le Quere C, Friedlingstein P, Tans PP (2000) Regional changes in carbon dioxide fluxes of land and oceans since 1980. *Science* 290:1342–1346
- Browder J, Godfrey B (eds) (1997) *Rainforest Cities—Urbanization, Development, and Globalization of the Brazilian Amazon*. Columbia University Press, New York
- Brown IF, Martinelli LA, Thomas WW, Moreira MZ, Ferreira CAC, Victoria RL (1995) Uncertainty in the biomass of Amazonian forests—an example from Rondonia, Brazil. *For Ecol Manag* 75(1–3):175–189
- Camargo PB, Trumbore SE, Martinelli LA, Davidson EA, Nepstad DC, Victoria RL (1999) Soil carbon dynamics in regrowing forest of eastern Amazonia. *Global Change Biol* 5:693–702
- Carswell FE, Costa AL, Palheta M, Malhi Y, Meir PW, Costa J de PR, Ruivo M de L, Leal LSM, Costa JMN, Clement RJ, Grace J (2002) Seasonality in CO<sub>2</sub> and H<sub>2</sub>O flux at an Eastern Amazonian rain forest. *J Geophys Res Atmos* 107(D20):8076. DOI 10.1029/2000JD000284
- Carvalho G, Barros AC, Moutinho P, Nepstad D. (2001) Sensitive development could protect Amazonia instead of destroying it. *Nature* 409:13
- Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO (1999) Changing sources of nutrients during four million years of ecosystem development. *Nature* 397(6719):491–497
- Chambers JQ, Higuchi N, Schimel JP (1998) Ancient trees in Amazonia. *Nature* 391(6663):135–136
- Chambers JQ, Higuchi N, Schimel JP, Ferreira LV, Melack JM (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia* 122:380–388
- Chambers JQ, Santos J, Ribeiro RJ, Higuchi N (2001a) Tree damage, allometric relationships, and above-ground net primary production in a tropical forest. *For Ecol Manag* 152:73–84
- Chambers JQ, Higuchi N, Tribuzy ES, Trumbore SE (2001b) Sink for a century: carbon sequestration in the Amazon. *Nature* 410(6827):429–429
- Chambers JQ, Silver WL (2004) Some aspects of ecophysiological and biogeochemical responses of tropical forests to atmospheric change. *Philos T Roy Soc B* 359(1443):463–476
- Chambers JQ, Tribuzy ES, Toledo LC, Crispim BF, Higuchi N, Santos J, Araújo AC, Kruijt B, Nobre AD, Trumbore SE (2004) Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecol Appl Suppl* 14(4):S72–S88
- Chambers JQ, Higuchi N, Teixeira LM, Santos J, Laurance SG, Trumbore SE (2004) Response of tree biomass and wood litter to disturbance in a central Amazon Forest. *Oecologia* 141:596–614
- Chave J, Condit R, Aguilar S, Hernandez A, Lao S, Perez R (2004) Error propagation and scaling for tropical forest biomass estimates. *Philos T Roy Soc B* 359(1443):409–420
- Chomovitz KM, Thomas TS (2001) Geographical patterns of land use and land intensity in the Brazilian Amazon. *Policy Research Working Paper* 2687, The World Bank
- Ciais P, Tans PP, White JWC, Trolier M, Francey RJ, Berry JA, Randall DR, Sellers PJ, Collatz JG, Schimel DS (1995) Partitioning of ocean and land uptake of CO<sub>2</sub> as inferred by  $\delta^{13}\text{C}$  measurements from the NOAA climate monitoring and diagnostics laboratory global air sampling network. *J Geophys Res* 100:5051–5070
- Claeys M, Graham B, Vas G, Wang W, Vermeylen R, Pashynska V, Cafmeyer J, Guyon P, Andreae MO, Artaxo P, Maenhaut W (2004) Formation of secondary organic aerosols through photo-oxidation of isoprene. *Science* 303:1173–1176
- Clark DA (2004) Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. *Phil Trans R Soc Lond B*. DOI 10.1098/rstb.2003.1426
- Clark DA (2002) Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecol Appl* 12:3–7
- Cochrane MA, Laurance WF (2002) Fire as a large-scale edge effect in Amazonian forests. *J Tropical Ecol* 18:1–15
- Cochrane MA, Alencar A, Schulze MD, Souza CM Jr, Nepstad DC, Lefebvre PA, Davidson EA (1999) Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* 284:1832–1835
- Condit R, Hubbell SP, Foster Rb (1995) Mortality-rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol Monogr* 65(4):419–439

- Conway TJ, Tans PP, Waterman LS, Thoning KW, Kitzis DR, Masarie KA, Zhang N (1994) Evidence for interannual variability of the carbon cycle from the National Oceanic and Atmospheric Administration/Climate Monitoring and Diagnostics Laboratory global air sampling network. *J Geophys Res* 99:22831–22855
- Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408:184–187
- Crutzen PJ, Fall R, Galbally I, Lindinger W (1999) Parameters for global ecosystem models. *Nature* 399:535–536
- Culf AD, Esteves JL, Marques Filho AO, Rocha HR (1996) Radiation, temperature and humidity over forest and pasture in Amazonia. In: Gash JHC, Nobre CA, Roberts JM, Victoria RL (eds) *Amazonian climate and deforestation*. Wiley, New York, pp 175–192
- Davidson EA, Verchot LV, Cattânio JH, Ackerman IL, Carvalho JEM (2000) Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry* 48:53–69
- DeFries RS, Houghton RA, Hansen MC, Field CB, Skole D, Townsend J (2002) Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. *PNAS* 99:14256–14261
- Dezzeo N, Worbes M, Ishii I, Herrera R (2003) Annual tree rings revealed by radiocarbon dating in seasonally flooded forest of Mapipe river (Orinoco river, Venezuela). *Plant Ecol* 168:165–175
- Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. *Science* 263:185–190
- Fan S, Gloor M, Mahlman J, Pacala S, Sarmiento J, Takahashi T, Tans P (1998) A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science* 282:442–446
- Fearnside PM (1996) Amazonian deforestation and global warming: carbon stocks in vegetation replacing Brazil's Amazon forest. *For Ecol Manag* 80:21–34
- Fearnside PM (1997) Greenhouse gases from deforestation in Brazilian Amazonia: net committed emissions. *Climatic Change* 35:321–360
- Fearnside PM (2000) Global warming and tropical land use change: greenhouse gas emissions from biomass burning, decomposition, and soils in forest conversion, shifting cultivation, and secondary vegetation. *Climatic Change* 46:115–158
- Field CB, Behrenfeld MJ, Randerson J, Falkowski (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237–240
- Friedlingstein P, Fung I, Holland E, John J, Brasseur G, Erickson D, Schimel D (1995) On the contribution of CO<sub>2</sub> fertilization to the missing biospheric sink. *Global Biogeochem Cy* 9(4):541–556
- Gash JHC, Huntingford C, Marengo JA, Betts RA, Cox PM, Fisch G, Fu R, Gandu AW, Harris PP, Machado LAT, von Randow C, Silva Dias MA (2004) Amazonian climate: results and future research. *Theor Appl Climatol (LBA Special Issue)* 78:187–193
- Gerwing JJ, Farias DL (2000) Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *J Trop Ecol* 16:327–335
- Goulden ML, Miller SD, Rocha HR, Menton MC, Freitas HC, Figueira AMS, Sousa CAD (2004) Diel and seasonal patterns of tropical forest CO<sub>2</sub> Exchange. *Ecol Appl Suppl* 14(4):S42–S54
- Goulden ML, Munger JW, Fan SM, Daube BC, Wofsy SC (1996) Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Global Change Biol* 2:168–182
- Grace J, Lloyd J, McIntyre J, Miranda AC, Meir P, Miranda HS, Nobre C, Moncrieff J, Massheder J, Malhi Y, Wright I, Gash J (1995a) Carbon dioxide uptake by an undisturbed tropical rain forest in Southwest Amazonia, 1992–1993. *Science* 270:778–780
- Grace J, Lloyd J, McIntyre J, Miranda AC, Meir P, Miranda HS, Moncrieff J, Massheder J, Wright I, Gash J (1995b) Fluxes of carbon dioxide and water vapor over an undisturbed tropical forest in south-west Amazonia. *Global Change Biol* 1:1–12
- Grace J, Malhi Y, Lloyd J, McIntyre J, Miranda AC, Meir P, Miranda HS (1996) The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. *Global Change Biol* 2:208–217
- Greenberg JP, Guenther AB, Petron G, Wiedinmyer C, Vega O, Gatti L, Tota J, Fisch G (2004) Biogenic VOC emissions from forested and cleared Amazonian landscapes. *Global Change Biol* 10(5):651–662
- Guenther A, Nicholas HC, Erickson D, Fall R, Geron C, Harley T, Graedel P, Klinger L, Pierce T, Taylor J (1995) A global model of natural volatile organic compound emissions. *J Geophys Res* 100:8873–8892
- Guenther A (2002) The contribution of reactive carbon emissions from vegetation to the carbon balance of terrestrial ecosystems. *Chemosphere* 49:837–844
- Gurney KR, Law RM, Denning AS, Rayner PJ, Baker D, Bousquet P, Bruhwiler L, Chen YH, Ciais P, Fan S, Fung IY, Gloor M, Heimann M, Higuchi K, John J, Maki T, Maksyutov S, Masarie K, Peylin P, Prather M, Pak BC, Randerson J, Sarmiento J, Taguchi S, Takahashi T, Yuen CW (2002) Towards robust regional estimates of CO<sub>2</sub> sources and sinks using atmospheric transport models. *Nature* 415(6872):626–630
- Harley P, Vasconcelos P, Vierling L, Pinheiro CS, Greenberg J, Guenther A, Klinger L, Almeida S, Neill D, Baker T, Phillips O, Malhi Y (2004) Variation in potential for isoprene emissions among Neotropical forest sites. *Global Change Biol* 10(5):630–650
- Hecht Sb (1993) The logic of livestock and deforestation in Amazonia. *Bioscience* 43(10):687–695
- Hirsch AI, Little WS, Houghton RA, Scott NA, White JD (2004) The net carbon flux due to deforestation and forest re-growth in the Brazilian Amazon: analysis using a process-based model. *Global Change Biol* 10(5):908–924. DOI 10.1111/j.1529-8817.2003.00765.x
- Hodnett MG, da Silva LP, Rocha HR, Cruz Senna RC (1995) Seasonal soil water storage changes beneath central Amazonian rainforest and pasture. *J Hydrol* 170:233–254
- Houghton RA (2003) Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. *Tellus* 55B:378–390
- Houghton RA, Lawrence KT, Hackler JL, Brown S (2001) The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. *Global Change Biol* 7:731–746
- Houghton RA, Skole DL, Nobre CA, Hackler JL, Lawrence KT, Chomentowski WH (2000) Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature* 403:301–304
- Houghton RA, Davidson EA, Woodwell GM (1998) Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance. *Global Biogeochem Cycles* 12(1):25–34
- House JI, Prentice IC, Ramankutty N, Houghton RA, Heimann M (2003) Reconciling apparent inconsistencies in estimates of terrestrial CO<sub>2</sub> sources and sinks. *Tellus* 55B:345–363
- INPE (Instituto Nacional de Pesquisas Espaciais) (2004) *Desflorestamento 1998–2004*. (<http://www.inpe.gov.br>) INPE, São José dos Campos, São Paulo, Brazil
- Ito A, Oikawa T (2000) A model analysis of the relationship between climate perturbations and carbon budget anomalies in global terrestrial ecosystems: 1970 to 1997. *Climate Res* 15:161–183
- Jarvis PG, Massheder JM, Hale SE, Moncrieff JB, Rayment M, Scott SL (1997) Seasonal variation of carbon dioxide, water vapor, and energy exchanges of a boreal black spruce forest. *J Geophys Res Atmos* 102(D24):28953–28966
- Johnson CM, Vieira ICG, Zarin DJ, Frizano J, Johnson AH (2001) Carbon and nutrient storage in primary and secondary forests in eastern Amazonia. *For Ecol Manag* 147:245–252

- Junk WJ (1997) The central Amazon floodplain: ecology of pulsing system. Springer, Berlin Heidelberg, p 525
- Keller M, Clark DA, Clark DB, Weitz AM, Veldkamp E (1996) If a tree falls in the forest. *Science* 273(5272):201
- Keller M, Palace M, Hurtt G (2001) Biomass estimation in the Tapajós National Forest, Brazil. Examination of sampling and allometric uncertainties. *For Ecol Manag* 154:371–382
- Kesselmeier J, Kuhn U, Wolf A, Andreae MO, Ciccioli P, Brancaleoni E, Frattoni M, Guenther A, Greenberg J, Vasconcellos PD, De Oliva ST, Tavares T, Artaxo P (2000) Atmospheric volatile organic compounds (VOC) at a remote tropical forest site in central Amazonia. *Atmos Environ* 34:4063–4072
- Kesselmeier J, Ciccioli P, Kuhn U, Stefani P, Biesenthal T, Rottenberger S, Wolf A, Vitullo M, Valentini R, Nobre A, Kabat P, Andreae MO (2002a) Volatile organic compound emissions in relation to plant carbon fixation and the terrestrial carbon budget. *Global Biogeochem Cycles* 16:1126. DOI 10.1029/2001GB001813
- Kesselmeier J, Kuhn U, Rottenberger S, Biesenthal T, Wolf A, Schebeske G, Andreae MO, Ciccioli P, Brancaleoni E, Frattoni M, Oliva ST, Botelho ML, Silva CMA, Tavares TM (2002b) Concentrations and species composition of atmospheric volatile organic compounds (VOCs) as observed during the wet and dry season in Rondonia (Amazonia) *J Geoph Res Atmos* 107(D20):8053
- Körner C (2004) CO<sub>2</sub> enrichment may cause tropical forests to become carbon sources. *Phil Trans R Soc Lond B*. DOI 10.1098/rstb.2003.1429
- Kruijt B, Elbers JA, von Randow C, Araujo AC, Oliveira PJ, Culf A, Manzi AO, Nobre AD, Kabat P, Moors EJ (2004) The robustness in eddy correlation fluxes for Amazon rainforest conditions. *Ecol Appl* 14:S101–S113
- Kuhn U, Rottenberger S, Biesenthal T, Wolf A, Schebeske G, Ciccioli P, Brancaleoni E, Frattoni M, Tavares TM, Kesselmeier J (2004) Seasonal differences in isoprene and light-dependent monoterpene emission by tropical tree species. *Global Change Biol* 10(5):663–682
- Kuhn U, Rottenberger S, Biesenthal T, Wolf A, Schebeske G, Ciccioli P, Brancaleoni E, Frattoni M, Tavares T, Kesselmeier J (2002) Isoprene and monoterpene emission of Amazonian tree species during the wet season: Direct and indirect investigations of controlling functions. *J Geophys Res Atmos* 107. DOI 10.1029/2001JD000978
- Laurance WF (2004) Forest–climate interactions in fragmented tropical landscapes. *Phil Trans R Soc Lond B*. DOI 10.1098/rstb.2003.1430
- Laurance WF, Cochrane MA, Bergen S, Fearnside PM, Delamonica P, Barber C, D'Angelo S, Fernandes T (2001) The future of the Brazilian Amazon. *Science* 291(5503):438–439
- Laurance WF et al (1997) Biomass collapse in Amazonian forest. *Science* 278:1117–1118
- Lloyd J, Bird MI, Veenendaal EM, Kruijt B (2001) Should phosphorus availability be constraining moist tropical forest responses to increasing CO<sub>2</sub> concentrations? In: Schulze ED (ed) *Global biogeochemical cycles in the climate system*. Academic, San Diego, pp 95–114
- Malhi Y, Baker T, Phillips OL, Almeida S, Alvarez E, Arroyo L, Chave J, Czimczik CI, DiFiore A, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Montoya LMM, Monteagudo A, Neill DA, Vargas PN, Patina S, Pitman NCA, Quesada CA, Silva JNM, Lezama AT, Martinez RV, Terborgh J, Vinceti B, Lloyd J (2004) The above-ground wood productivity and net primary productivity of 100 neotropical forest plots. *Global Change Biol* 10(5):563–591
- Malhi Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests. *Plant Cell Environ* 22:715–740
- Malhi Y, Grace J (2000) Tropical forests and atmospheric carbon dioxide. *Trends Ecol Evol* 15:332–337
- Malhi Y, Nobre AD, Grace J, Kruijt B, Pereira MGP, Culf A, Scott S (1998) Carbon dioxide transfer over a central Amazonian rain forest. *J Geophys Res Atmos* 103:31593–31612
- Malhi Y, Wright J (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. *Phil Trans R Soc Lond B*. DOI 10.1098/rstb.2003.1433
- Manzi AO et al (2002) NEE over a floodable ecosystem in Pantanal, Brazil, II LBA Scientific Conference, Manaus
- Marengo JA, Nobre CA (2001) General characteristics and variability of climate in the Amazon basin and its links to the global climate system. In: McClain ME, Victoria RL, Richey JE (eds) *The biogeochemistry of the Amazon basin*. Oxford University Press, New York
- Margulis S (2003) Causes of Deforestation of the Brazilian Amazon. World Bank working paper no. 22
- McGuire AD, Melillo JM, Kicklighter DW, Pan YD, Xiao XM, Helfrich J, Moore B, Vorosmarty CJ, Schloss AL (1997) Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: sensitivity to changes in vegetation nitrogen concentration. *Global Biogeochem Cycles* 11(2):173–189
- Melillo JM, Houghton RA, Kicklighter DW, McGuire AD (1996) Tropical deforestation and the global carbon budget. *Annu Rev Energy Environ* 21:293–310
- Melillo JM, McGuire AD, Kicklighter DW, Moore B III, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. *Nature* 363:234–240
- Miller SD, Goulden ML, Menton MC, Rocha HR, Freitas HC, Figueira AMS, Sousa CAD (2004) Biometric and micrometeorological measurements of tropical forest carbon balance. *Ecol Appl* 14(4):S114–S126
- Miranda AC, Miranda HS, Lloyd J, Grace J, McIntyre JA, Meir P, Riggan P, Lockwood R, Brass J (1996) Carbon dioxide fluxes over a cerrado *sensu stricto* in central Brazil. In: Gash JHC, Nobre CA, Roberts JM, Victoria RL (eds) *Amazonian climate and deforestation*. Wiley, New York, pp 353–364
- Miranda EV (2002) Padrão de desenvolvimento radial horário de tres especies arboreas da Amazonia utilizando dendrometros automaticos. MSc Dissertation, INPA, Manaus
- Martens CS, Shay TJ, Mendlovitz HP, Matross DM, Saleska SR, Wofsy SC, Woodward WS, Menton MC, De Moura JMS, Crill PM, De Moraes OLL, Lima RL (2004) Radon fluxes in tropical forest ecosystems of Brazilian Amazonia: night-time CO<sub>2</sub> net ecosystem exchange derived from radon and eddy covariance methods. *Global Change Biol* 10(5):618. DOI 10.1111/j.1365-2486.2004.00764.x
- Nelson BW, Mesquita R, Pereira JLG, de Souza SGA, Batista GT, Couto LB (1999) Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. *For Ecol Manag* 117:149–167
- Nepstad D, McGrath D, Alencar A, Barros AC, Carvalho G, Santilli M, Diaz M del CV (2002) Frontier governance in Amazonia. *Science* 295:629–631
- Nepstad DC, Carvalho GO, Barros AC, Alencar A, Capobianco JP, Bishop J, Moutinho P, Lefebvre PA, Silva UL, Prins E (2001) Road paving, fire regime feedbacks, and the future of Amazon forests. *For Ecol Manag* 154:395–407
- Oliveira AA, Nelson BW (2001) Floristic relationship of terra firme forests in the Brazilian Amazon. *For Ecol Manag* 146:169–197
- Phillips OL, Gentry AH (1994) Increasing turnover through time in tropical forests. *Science* 263:954–958
- Phillips OL, Malhi Y, Higuchi N, Laurance WF, Núñez PV, Vásquez RM, Laurance SG, Ferreira LV, Stern M, Brown S, Grace J (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282:439–442
- Phillips OL, Malhi Y, Vinceti B, Baker T, Lewis SL, Higuchi N, Laurance WF, Vargas PN, Martinez RV, Laurance S, Ferreira LV, Stern M, Brown S, Grace J (2002a) Changes in growth of tropical forests: evaluating potential biases. *Ecol Appl* 12:576–587
- Phillips OL, Martinez RV, Arroyo L, Baker TR, Killeen T, Lewis SL, Malhi Y, Mendoza AM, Neill D, Vargas PN, Alexiades M, Ceron C, Di Fiore A, Erwin T, Jardim A, Paaiacios W, Saidias M, Vinceti B (2002b) Increasing dominance of large lianas in Amazonian forests. *Nature* 418:770–774



- Phillips O, Baker T, Arroyo L, Higuchi N, Killeen T, Laurance WF, Lewis SL, Lloyd J, Malhi Y, Monteagudo A, Neill D, Nunez Vargas P, Silva N, Terborgh J, Vasquez Martnez R, Alexiades M, Almeida S, Brown S, Chave J, Comiskey JA, Czimczik CI, Di Fiore A, Erwin T, Kuebler C, Laurance SG, Nascimento HEM, Olivier J, Palacios W, Patino S, Pitman N, Quesada CA, Saldias M, Torres Lezama A, Vinceti B (2004) Pattern and process in Amazon tree turnover, 1976–2001. *Phil Trans R Soc Lond B*. DOI 10.1098/rstb.2003.1438
- Piedade MTF, Junk WJ, Parolin P (2000) The flood and photosynthetic response of trees in a White water floodplain (várzea) of the Central Amazon, Brazil. *Verh Int Verein Limmol* 27:1734–1739
- Prentice IC, Farquhar GD, Fasham MJR, Goulden ML, Heimann M, Jaramillo VJ, Khesghi HS, Le Quere C, Scholes RJ, Wallace DWR (2001) The carbon cycle and atmospheric carbon dioxide. In: Houghton JT (ed) *Climate change 2001: the scientific basis*. Cambridge University Press, Cambridge, pp 183–237
- Procópio AS, Artaxo P, Kaufman YJ, Remer LA, Schafer J S, Holben BN (2004) Multiyear analysis of Amazonian biomass burning smoke radiative forcing of climate. *Geophys Res Lett* 31:L03108. DOI 10.1029/2003GL018646
- Rice AH, Pyle EH, Saleska SR, Hutrya L, Carmargo PB, Portilho K, Marques DF, Wofsy SF (2004) Carbon balance and vegetation dynamics in an old growth Amazonian forest. *Ecol Appl* 14(4):555–571
- Richey JE, Melack JM, Aufdenkampe AK, Ballester VM, Hess LL (2002) Outgassing from Amazonian rivers and wetlands as a large tropical source of atmospheric CO<sub>2</sub>. *Nature* 416:617–620
- Rocha HR, Freitas H, Rosolem R, Juarez R, Tannus RN, Ligo MV, Cabral OMR, Silva Dias MAF (2002) Measurements of CO<sub>2</sub> exchange over a woodland savanna (Cerrado Sensu stricto) in southeast Brazil. *Biota Neotropica* 2(1):
- Rocha HR, Goulden ML, Miller SD, Menton MC, Pinto LDVO, Freitas HC, Figueira AMS (2004) Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia. *Ecol Appl Suppl* 14(4):S22–S32
- Sakai R, Fitzjarrald D, Moraes O, Staebler R, Acevedo O, Czirkowsky M, da Silva R, Brait E, Miranda V (2004) Land-use effects on local energy, water and carbon balances in an Amazonian agricultural field. *Global Change Biol* 10(5):895–907
- Saleska SR, Miller SD, Matross DM, Goulden ML, Wofsy SC, da Rocha HR, de Camargo PB, Crill P, Daube BC, de Freitas HC, Hutrya L, Keller M, Kirchoff V, Menton M, Munger JW, Pyle EH, Rice AH, Silva H (2003) Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. *Science* 302:1554–1557
- Schimel DS, House JI, Hibbard KA, Bousquet P, Ciais P, Peylin P, Braswell BH, Apps MJ, Baker D, Bondeau A, Canadell J, Churkina G, Cramer W, Denning AS, Field CB, Friedlingstein P, Goodale C, Heimann M, Houghton RA, Melillo JM, Moore III B, Murdiyarso D, Noble I, Pacala SW, Prentice IC, Raupach MR, Rayner PJ, Scholes RJ, Steffen WL, Wirth C (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* 414:169–172
- Schimel DS (1995) Terrestrial ecosystems and the carbon-cycle. *Global Change Biol* 1:77–91
- Schongart J, Junk W, Piedade MTF, Ayres M, Alloy Shutterman A, Worbes M (2004) Teleconnection between tree growth in the Amazonian floodplains and the El Niño–Southern Oscillation effect. *Global Change Biol* 10:1–10
- Schongart J, Piedade MTF, Ludwigshausen S, Horna V, Worbes M (2002) Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. *J Trop Ecol* 18:581–597
- Silva Dias MAF, Rutledge S, Kabat P, Silva Dias PL, Nobre C, Fisch G, Dolman AJ, Zipser E, Garstang M, Manzi A, Fuentes JD, Rocha H, Marengo J, Plana-Fattori A, Sá L, Alvalá R, Andreae M O, Artaxo P, Gielow R, Gatti L (2002) Clouds and rain processes in a biosphere atmosphere interaction context in the Amazon region. *J Geophys Res*. DOI 10.1029/2001JD000335
- Silva RP, Santos J, Tribuzy ES, Chambers JQ, Nakamura S, Higuchi N (2002) Diameter increment and growth patterns for individual trees in Central Amazon, Brazil. *For Ecol Manag* 116:295–301
- Staebler RM, Fitzjarrald DR (2004) Observing subcanopy CO<sub>2</sub> advection. *Agric For Met* 122(3–4):139–156
- Tans PP, White JWC (1998) The global carbon cycle—In balance, with a little help from the plants. *Science* 281(5374):183–184
- Tans PP, Fung IY, Takahashi T (1990) Observational constraints on the global atmospheric CO<sub>2</sub> budget. *Science* 247:1431–1438
- Telles ECC, de Camargo PB, Martinelli LA, Trumbore SE, da Costa ES, Santos J, Higuchi N, Oliveira RO Jr (2003) Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia. *Global Biogeochemical Cycles* 17:1040. DOI 10.1029/2002GB001953
- Thomaz WW (2000) Conservation and monographic research on the flora of tropical America. *Biodivers Conserv* 8:1007–1015
- Thompson MV, Randerson JT, Malmstrom CM, Field CB (1996) Change in net primary production and heterotrophic respiration: how much is necessary to sustain the terrestrial carbon sink? *Global Biogeochem Cy* 10(4):711–726
- Tian H, Melillo JM, Kicklighter DW, McGuire AD, Helfrich III J, Moore III B, Vorosmarty CJ (2000) Climatic and biotic controls on annual carbon storage in Amazonian ecosystems. *Global Ecol Biogeogr* 9:315–335
- Tuomisto H, Ruokolainen K, Kalliola R, Linna A, Danjoy W, Rodriguez Z (1995) Dissecting Amazonian biodiversity. *Science* 269:63–66
- Victoria RL, Martinelli LA, Moraes JM, Ballester MV, Krusche AV, Pellegrino G, Almeida RMB, Richey JE (1998) Surface air temperatures variations in the Amazon region and its borders during this century. *J Climate* 11:1105–1110
- Vieira S, Camargo PB, Selhorst D, Silva R, Hutrya L, Chambers JQ, Brown IF, Higuchi N, Santos J, Wofsy S, Trumbore SE, Martinelli LA (2004) Forest structure and carbon dynamics in Amazonian tropical rain forest. *Oecologia*. DOI 10.1007/s00442-004-1598-z
- Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65:285–298
- Vitousek PM, Sanford RL (1986) Nutrient cycling in moist tropical forests. *An Rev Ecol Syst* 17:137–168
- von Randow C, Sá LDA, Prasad GSSD, Manzi A, Kruijt B (2001) Scale variability of surface fluxes of energy and carbon over a tropical rain forest in South-West Amazonia. I. Diurnal Conditions. *J Geophys Res* 107. DOI 10.1029/2001JD000379
- Vourlitis GL, Priante Filho N, Hayashi MMS, Nogueira JS, Raiter F, Hoegel W, Campelo Jr JH (2004) The role of seasonal variations in meteorology on the net CO<sub>2</sub> exchange of a Brazilian transitional tropical forest. *Ecol Appl Suppl* 14(4):S89–S100
- Vourlitis GL, Priante-Filho N, Hayashi MMS, Nogueira JS, Caseiro FT, Campelo JH (2001) Seasonal variations in the net ecosystem CO<sub>2</sub> exchange of a mature Amazonian tropical transitional forest (cerradão). *Funct Ecol* 15:388–395
- Walker R, Moran E, Anselin L (2000) Deforestation and cattle ranching in the Brazilian Amazon: external capital and household processes. *World Dev* 28(4):683–699
- Williams E, Madden N, Rosenfeld D, Gerlach J, Atkinson L, Dunnemann N, Frostrom G, Gears N, Antonio M, Biazon B, Camargo R, Franoa H, Gomes A, Lima M, Machado R, Manhaes S, Nachtigall L, Piva H, Quintiliano W, Machado L, Artaxo P, Roberts G, Renno N, Blakeslee R, Bailey J, Boccippio D, Betts A, Wolff D, Roy B, Halverson J, Rickenbach T, Fuentes J, Avelino E (2002) Contrasting convective regimes over the Amazon: implications for cloud electrification. *J Geophys Res* 107(D20):50.1–50.19

- White A, Cannell MGR, Friend AD (2000) CO<sub>2</sub> stabilization, climate change and the terrestrial carbon sink. *Global Change Biol* 6:817–833
- Wiedinmyer C, Guenther A, Harley P, Hewitt N, Geron C, Artaxo P, Steinbrecher R, Rasmussen R (2004) Global organic emissions from vegetation. In: Granier C, Artaxo P, Reeves C (eds) *Emissions of trace gases and aerosols into the atmosphere*. Kluwer, Dordrecht
- Worbes M (2002) One hundred years of tree ring research in the tropics. A brief history and an outlook to future challenges. *Dendrochronologia* 20(1–2):217–231
- Wright IR, Gash JHC, da Rocha HR, Shuttleworth WJ, Nobre CA, Maitelli GT, Zamparoni CAGP, Carvalho PRA (1992) Dry season micrometeorology of central Amazonian ranchland. *Q J Roy Meteorol Soc* 118:1083–1099