

The Regional Carbon Budget

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A number of approaches have been used to infer whether Amazonia is a net source or sink for carbon. Top-down approaches based on inverse calculations with CO₂ concentrations and atmospheric transport models are problematic because of a paucity of air samples and poor constraints on regional air transport. Direct measurements of changes in aboveground biomass suggest a net carbon sink in old-growth forests but remain controversial. Direct measurements of CO₂ flux with the eddy covariance technique indicate forests to be both sources and sinks of carbon, depending in part on when the last disturbance occurred. These flux measurements may be extrapolated through time and space with ecosystem models based on physiological processes, but many models fail to reproduce even the correct sign of carbon balance observed seasonally in some forests. Models based on changes in forest structure, driven by both anthropogenic (e.g., deforestation for pasture) and natural (e.g., fire) disturbances and recovery, consistently calculate net carbon emissions, emissions that may be offset by the increased biomass observed in long-term plots in old-growth forests. Aquatic systems are nearly neutral with respect to carbon, with inputs from seasonally flooded forests and grasslands accounting for the measured efflux. Taken together, these different approaches, which often consider different components of the region's carbon cycle, suggest that Amazonia has been, on average, nearly neutral with respect to carbon over the last decade, albeit a small net source during El Niño events.

1. INTRODUCTION

This chapter is concerned with two questions: What is the carbon balance of Amazonia, and why (i.e., What are the processes responsible for sources and sinks of carbon in the region)? The processes fall into two broad categories. The

first category includes metabolic or physiological processes, photosynthesis, respiration, decomposition, water relations, processes that respond to environmental drivers, such as light, moisture, temperature, CO₂ concentrations, and nutrients. The second broad category of processes includes disturbances and recovery, including both direct anthropogenic effects (e.g., deforestation for pasture) and natural or indirect anthropogenic effects (e.g., fire).

In addressing whether Amazonia is a source or sink for carbon, the chapter looks first at results from two atmospheric-based approaches: (1) inverse calculations based on spatial and temporal variations in atmospheric CO₂ concentrations and models of atmospheric transport and (2) atmospheric air column carbon budgets based on vertical profiles of CO₂ over the region. The results of these approaches are ambiguous with respect to whether Amazonia is a net source or sink for carbon.

Subsequent sections consider ground-based measurements: measurements of CO₂ flux by eddy covariance, long-term measurements of forest biomass on permanent plots, and measurement of carbon dynamics in aquatic systems. Although the results of eddy covariance measurements are difficult to extrapolate over large regions, they are useful for constructing process-based physiological models that, in turn, are used to estimate sources and sinks of carbon in response to environmental variables. Models are also used to calculate the sources and sinks of carbon that result from disturbances and recovery.

In the last section, we bring together the results of the observations and models to answer the two questions posed: What is the net carbon balance? and What are the mechanisms responsible? More specifically, we seek to identify and quantify the sources and sinks of carbon attributable to metabolic responses to environmental change, and those attributable to disturbance and recovery processes.

2. CARBON BALANCE OF AMAZONIAN REGIONS: ESTIMATES FROM THE ATMOSPHERE

2.1. Global Estimates From Inverse Calculations: What Do Atmospheric Concentration Data Tell Us About the Carbon Balance of Amazonia?

There have been numerous studies in which large-scale carbon fluxes are inferred from atmospheric concentration data and inverse modeling of atmospheric transport, but the underlying inversion methods vary substantially, and the results are conflicting. The basic principle of the approach is to infer surface fluxes from the accumulation or depletion of CO₂ in the air above the region of interest. If air motion acting on the CO₂ concentration field can be determined, it

should be possible to infer surface flux strength, location, and time course. Atmospheric transport can be simulated fairly realistically by numerical integration of the transport equation with data derived from regular worldwide observations of the state of the atmosphere (e.g., winds, air masses). Nonetheless, these models are not perfect. Particularly problematic is the representation of processes operating at smaller spatial scales than the scale used for the discretization of the transport equation [e.g., Peters *et al.*, 2004; Gloor *et al.*, 2007].

Atmospheric concentrations of CO₂ are currently measured at approximately 50 stations operated by NOAA's CMD and at a smaller number of other measurement networks run by CSIRO Division (Australia), University of Heidelberg (Germany), (University of Tokyo, National Institute for Environmental Studies (NIES) (Tsukuba, Japan), Laboratoire des Sciences du Climat et de l'Environnement (France), and Max-Planck Institute for Biogeochemistry (Germany). Until the end of the year 2000, these regular measurements were predominantly in remote locations at the earth's surface. The station locations were chosen to avoid large and rapidly varying fluxes, such as those due to photosynthesis and respiration on land and those due to fossil fuel burning and cement manufacture. Another traditional limitation of atmospheric concentration sampling has been the lack of information in the vertical dimension, which is not only necessary to characterize the CO₂ field but also essential to validate and calibrate model transport. In recognition of these shortcomings, dense vertical profile and tall tower continuous sampling have been initiated in the last few years over the United States, Europe, Japan, Russia, and, to a limited extent, over South America. As these data are very recent, their implications are only now being investigated, as discussed below. While enormous progress has been made in expanding the number of air sampling stations, important gaps in the network remain, most notably in tropical land regions where sampling is still very sparse.

Generally, the weaknesses in the approach of atmospheric inversions explaining the range in estimates are the following: (1) Flux estimates tend to be highly sensitive to biases and uncertainties in data and modeled transport. (2) The atmosphere has been and still is under-sampled. (3) Data to calibrate transport in models have been and still are sparse. (4) The covariation of transport and surface fluxes (the "rectifier effect") [Denning *et al.*, 1995] is a major uncertainty in these analyses.

Because tropical data are very sparse and thus resolution of different land regions in the tropics is hardly possible, we focus primarily on estimates of flux for tropical land as a whole instead of the Amazon Basin (or tropical South America).

Early studies by *Keeling et al.* [1989] and *Tans et al.* [1990] came to the conclusion that there is a substantial sink in Northern Hemisphere midlatitudes. *Keeling et al.* [1989] attributed the sink to the oceans, while *Tans et al.* [1990] attributed it to land. Independent estimates of air-sea flux at that time were quite uncertain. Subsequent studies were inconclusive [*Fan et al.*, 1998; *Bousquet et al.*, 2000], and a community effort was initiated to assess the model dependence of inverse-based flux estimates. This effort (Atmospheric Tracer Transport Model Intercomparison Project (TRANSCOM3)) resulted in an often cited publication [*Gurney et al.*, 2002]. Following the *Fan et al.* 1998, 1999 studies, air-sea flux priors (defined below) were based on compilations of partial pressure differences and a bulk gas exchange formulation [*Takahashi et al.*, 1999]. While this was probably the best that could be done at the time, global bulk exchange parameterizations are inherently uncertain. The use of priors, or prior information, is one approach for reducing uncertainties in the approach. As long as prior guesses are based on data and uncertainty variance-covariance can be rationally estimated, this approach is reasonable. However, often, regularization using prior estimates has not followed these principles.

Since the study of *Gurney et al.* [2002], the field has seen several advances. One was the estimation of air-sea gas fluxes and patterns based on ocean interior data and models [*Gloor et al.*, 2003; *Mikaloff-Fletcher et al.*, 2007]. A second initiated atmospheric sampling of the troposphere up to 8 km height over continents, mainly in Northern Hemisphere midlatitudes (North American Carbon Plan, Aerocarb, NIES Tsukuba). Furthermore, in recognition of the rectification problem (see point 4 above) and because of interest in the interannual variation in the atmospheric growth rate, inverse modeling studies started to resolve fluxes on monthly and shorter timescales [*Rayner et al.*, 1999; *Bousquet et al.*, 2000; *Rödenbeck et al.*, 2003; *Baker et al.*, 2006] (TRANSCOM3 level 2 intercomparison study). The next advance in methodology was the analysis by *Jacobson et al.* [2007], which combined ocean interior and atmospheric data in a coupled annual mean inversion using the entire 12-model suite of atmospheric inverse models from TRANSCOM3.

The final study we refer to here is that of *Stephens et al.* [2007], which assessed the implications of vertical profile measurements over the continents (predominantly Northern Hemisphere) using the TRANSCOM3 level 2 simulations and results. Based on these new data, *Stephens et al.* [2007] were able to select a subset of transport models from the TRANSCOM3 level 2 model suite that simulated existing CO₂ vertical profiles most closely. The fluxes estimated by the subset of selected models differs from the TRANSCOM3 level 2 mean (Table 1). In our compilation (Table 1), we also

report the TRANSCOM3 level 1 results for the subgroup of models selected by the *Stephens et al.* study, results which actually shed a somewhat different light on the published results of *Stephens et al.* [2007].

Before discussing the carbon balance estimates, themselves, we note that there is substantial interannual variation of fluxes between tropical lands and the atmosphere (Figure 1). It is noteworthy that South America seems to dominate the global interannual variability in the atmospheric growth rate, at least according to the *Rödenbeck et al.* [2003] study. Furthermore, these interannual flux “anomalies” are related to climate anomalies associated with El Niño–Southern Oscillation (ENSO), particularly over the Amazon Basin. Independent evidence for large variations in the fluxes from tropical land come from atmospheric CO, CH₄, and H₂ data [e.g., *Langenfelds et al.*, 2002].

The large interannual variability of these fluxes, closely associated with the ENSO, implies that an adequate budgeting period should include several El Niño/La Niña phases. Unfortunately, this last requirement is only partially fulfilled by the inversion studies discussed here (Table 1). All of these studies cover the period from January 1992 to December 1996 (the study of *Rödenbeck et al.* [2003] also covers the period from January 1996 to December 1999). As shown in Figure 1, the period contains both an El Niño and a La Niña phase. Thus, the estimates are likely not to be dominated by either of the two but rather provide a “climatological” mean.

According to the study of *Gurney et al.* [2002], based on 12 different models and annual means, there is a substantial Northern Hemisphere land sink, while tropical lands, including the Amazon Basin, release significant amounts of carbon to the atmosphere. The study of *Jacobson et al.* [2007] finds generally similar results, a strong Northern Hemisphere sink, and a statistically significant source from tropical and Southern Hemisphere land combined. This is not surprising as both studies used the same suite of 12 transport models from TRANSCOM3 level 1 (there are three TRANSCOM3 levels; level 1 calculations use annual mean data to estimate annual mean fluxes; level 2 calculations use monthly data to estimate monthly fluxes; level 3 calculations are, except for the fixed time period, “open protocol,” i.e., the inversion method and data selection are selected by the investigator). The flux from the study of *Jacobson et al.* [2007] may be considered to have more weight, however, as more realistic air-sea fluxes were used and no priors on land fluxes were employed.

The other studies come to somewhat different conclusions. The analysis by *Stephens et al.* [2007] described above, reduced the 12-model TRANSCOM3 suite to the 3 models that seem to exhibit the least transport biases. This model selection implies a slightly reduced source in the tropics and a

Table 1. Breakup of Land-Atmosphere Flux Estimates Into Three Zonal Bands From a Range of Atmospheric Transport Inversion Studies^a

	<i>Gurney et al.</i> [2002]	<i>Jacobson et al.</i> [2007]	<i>Rödenbeck et al.</i> [2003]		<i>Baker et al.</i> [2006]	<i>Stephens et al.</i> [2007]	
	1992–1996	1992–1996	1992–1996	1996–1999	1992–1996	1992–1996	
	12 Models T3L1	12 Models T3L1	<i>Transport Model</i>		12 Models {TM3, UCI, JMA} T3L2	T3L1 ^b	TM3 T3L2 ^c
			<i>Atmosphere Land Flux</i>				
S Hem (<20S)	-0.2 ± 1.1 (0.15)	-2.4 ± 2.0	0.0 ± 0.2 ()	0.1 ± 0.2 ()	-1.2	0.1 ± 1.1	
Tropics	1.1 ± 1.3 (1.5)	4.2 ± 2.7	-1.0 ± 0.4 ()	-0.8 ± 0.4 (0.3)	1.6	0.7 ± 1.4	-0.1 ± 0.8 1.0 (0.2)
N Hem (>20N)	-2.3 ± 0.6 (-0.7)	-2.9 ± 1.0	-0.7 ± 0.2 ()	-0.4 ± 1.0 ()	-2.7	-2.2 ± 0.6	-1.5 ± 0.6 -2.2 (0.8)
	-1.4	-1.1	-1.8	-1.3	-2.3	-1.4	
			<i>Atmosphere Ocean Flux</i>				
S Hem (<20S)	-0.8 ± 0.7 (0.0)	-1.4 ± 0.1	-1.0 ± 0.1 ()	-1.2 ± 0.2 ()	-0.7	-1.1 ± 0.7	
Tropics	0.4 ± 0.7 (0.0)	0.8 ± 0.1	0.9 ± 0.2 ()	1.1 ± 0.2 ()	0.7	0.4 ± 0.7	
N Hem (>20N)	-1.1 ± 0.5 (0.0)	-1.1 ± 0.1	-1.6 ± 0.1 ()	-1.7 ± 0.1 ()	-1.0	-0.7 ± 0.6	
	-1.5	-1.7	-1.7	-1.8	-1.0	-1.4	
Total	-2.9	-2.8	-3.5	-3.3	-3.3	-2.9	

^aValues are given in Pg C a⁻¹. The sign convention is that a positive flux is directed to the atmosphere. Numbers in brackets are a priori prescribed fluxes used in those inversions which use Bayesian priors to regularize the calculations. Empty parentheses indicate that prior fluxes have been used but cannot be inferred from the publication in question. TM3, UCI, and JMA stand for specific tracer transport models [see *Gurney et al.*, 2002], T3L1 stands for the TRANSCOM level 1 experiment results (based on annual mean data), and T3L2 stands for TRANSCOM level 2 results (based on monthly mean data). *Stephens et al.* [2007] determined a subset of transport models most compatible with recent vertical profile data not included in TRANSCOM inversions. We report on the results from this subset as well as for the transport model TM3 alone and with both T3L1 and T3L2.

^bCalculated by Gloor from *Gurney et al.* [2003].

^cSouthern Hemisphere fluxes are missing because *Stephens et al.* [2007] report only land flux estimates for Tropics and Northern Hemisphere (see p. 1734).

reduced northern midlatitude sink when focusing on annual mean inversions (TRANSCOM3 level 1). In contrast, when applying the same selection criterion to the TRANSCOM3 level 2 model suite (which resolve fluxes monthly instead of annually), tropical lands were carbon neutral with the Northern Hemisphere land sink strongly reduced. This result is qualitatively similar to that found by the other inversion study that used monthly inversions [*Rödenbeck et al.*, 2003], except the latter suggested a larger tropical land sink.

It thus seems that results from annual mean inversions differ from inversions that solve for monthly fluxes with or without model selection based on new vertical profile data. One reason is likely the role played by the rectification term applied in annual mean inversions (while not applied in monthly inversions). In contrast, the difference between

results based on monthly versus annual mean inversions does not seem to be so much related to the specific transport model used. Annual inversions based on the transport model TM3 differ markedly from the monthly mean inversion results based on the same model. In summary, the balance of Northern Hemisphere versus tropical land sinks, and thus the Amazon carbon balance provided by the atmospheric concentration constraint, remains inconclusive.

The recent new vertical profile data permit not only traditional inverse modeling but also a much simpler direct approach which makes more direct use of the main constraint provided by the atmosphere: the accumulation of constituents within an air volume above a surface source. This more direct approach simply balances inflow and outflow of air into the total air volume above the region in question

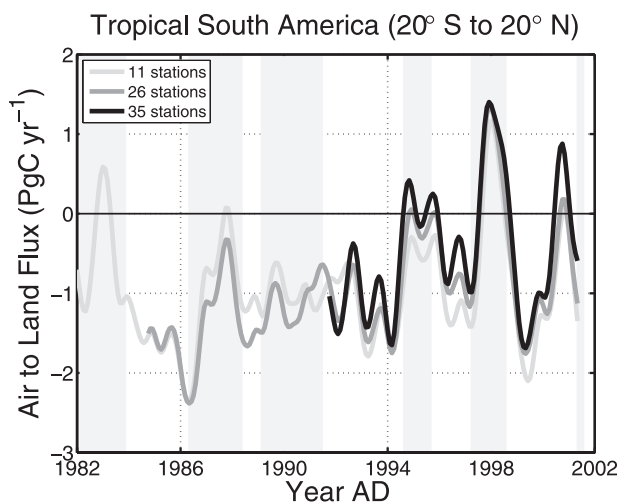


Figure 1. Estimate of fluxes to and from tropical South America to the atmosphere, based on atmospheric data and inverse modeling by Rödenbeck *et al.* [2003]. The different shadings correspond to estimates based on different station networks with records that cover the entire period for which fluxes are being estimated.

[Crevoisier *et al.*, 2006]. The method makes use of the flux-integrating property of the atmosphere and is insensitive to vertical transport biases and rectification, unlike traditional inverse transport modeling. It has recently been applied to North America (Crevoisier *et al.*, Robust carbon balance of contiguous North America 2004–2006 based on novel atmospheric data and methods, in preparation) as part of the North American Carbon Plan. In our view, this provides evidence that the flux integrating property of the atmosphere can be successfully exploited. However, this is only true if adequate vertical profile data are available. Some 5–10 regular vertical profile sites across Amazonia, complemented by surface reference stations along the western coastline, would be needed.

2.2. Regional Estimates

From repeated measurements of CO₂ concentrations within and above the atmospheric boundary layer, it is possible to derive the net surface fluxes of reasonably large areas of order 1000 km² [Wofsy *et al.*, 1988; Raupach *et al.*, 1992; Raupach and Finnigan, 1995; Kuck *et al.*, 2000; Lloyd *et al.*, 2001, 2007; Laubach and Frisch, 2002]. Variants of this technique have now been applied on four occasions to obtain estimates of the regional carbon balance for Amazonia: by using tethered balloon profiles [Culf *et al.*, 1999;

Kuck *et al.*, 2000]; by considering diurnal differences in the shape and integrated values of vertical CO₂ profiles from airborne measurements, even when made on different days [Chou *et al.*, 2002]; and by undertaking planned sequences of flights and analysing the vertical CO₂ profiles obtained in conjunction with model-derived estimates of other important parameters known to influence the derived surface fluxes, such as the net vertical velocity of the air masses occurring at the times of measurement and a consideration of potential advective effects [Lloyd *et al.*, 2007].

In all cases, analyses have been limited to periods of days or months with the validity of any conclusions also unclear because of methodological considerations and a requirement to make assumptions of unknown validity. For example, Chou *et al.* [2002] interpreted both the overall magnitude and diurnal pattern of their CO₂ balance calculations from a reanalysis of historical aircraft measurements over Amazonia as indicating a significant influence of net CO₂ emissions from wetlands, rivers, and inundated forest. Nevertheless, that conclusion required the assumption that a uniform temporal pattern of daytime convection existed so as not to bias their interpretation of the diurnal changes in many different vertical CO₂ profiles observed over many different days. Nevertheless, convective activity is generally at its greatest in the afternoon/evening [Machado *et al.*, 2002, 2004], thereby often tending to “reset” profiles [Lloyd *et al.*, 1996] allowing for a new cycle in atmospheric [CO₂] to commence from a different start point to before the storm. Once a convective event has occurred (more or less dissipating any vertical gradient in CO₂), the effects of that convective event should continue to be observed in all CO₂ profiles observed for the same air mass over the remainder of the day (or until the next convective event).

Likewise, the study of Kuck *et al.* [2000] ignored any possible vertical velocity effects, and even when such estimates are made, these inevitably come from model output rather than direct measurements, with any errors in the values used having potentially large effects on the fluxes so derived [Lloyd *et al.*, 2001, 2007].

Nevertheless, even after such errors in derived fluxes are taken into account, the airborne budgeting approach can prove useful, for example, in checking the validity of tower-based estimates of ecosystem carbon balances; the study of Lloyd *et al.* [2007], for example, showed that a significant underestimation of nighttime effluxes of carbon using the eddy covariance technique was occurring for two towers located above evergreen tropical forest near Manaus (see section 3.2). Kuhn *et al.* [2007] also applied aircraft data to help evaluate regional estimates of surface isoprene fluxes and associated atmospheric chemistry reaction parameters in the surface boundary layer.

3. CARBON BALANCE OF INTACT FORESTS

Several estimates of the carbon balance of Amazonian forest and cerrado have been made over the last 15 or so years with two primary methods employed: continuous and direct measurements of carbon fluxes using the eddy covariance technique [Grace *et al.*, 1995a, 1995b, 1996; Miranda *et al.*, 1996; Malhi *et al.*, 1998; Carswell *et al.* 2002; Santos *et al.*, 2003; Saleska *et al.*, 2003; Hutyra *et al.*, 2007] and estimates of rate of net aboveground biomass change from repeated censuses of permanent sample plots [Phillips *et al.*, 1998; Baker *et al.*, 2004; Lewis *et al.*, 2006]. However, these two approaches to determining the net carbon balance of individual forest or savanna stands, both of which involve the sampling of an area of approximately 1 ha, have proved controversial. Concerns have been raised with respect to methodological issues [Clark, 2002; Saleska *et al.*, 2003; Wright, 2005] and with the validity of extrapolating results of such studies to estimate the carbon balance of the Amazon Basin as a whole [Saleska *et al.*, 2003; Chambers and Silver, 2004; Chambers *et al.*, 2004; Wright, 2005]. Central to the latter criticism is the notion that all forests studied are recovering either from some unspecific (and thus hypothetical) small scale but regular disturbance [Chambers *et al.*, 2004] or from severe, widespread mortality events [Wright, 2005], such as may have occurred in the great Amazon drought of 1926 [Williams *et al.*, 2005], or earlier [Keller *et al.*, 1996].

3.1. Quantification of Stand Level Carbon Balances

The net carbon balance of any given area of vegetation and soil can be written as

$$\frac{dC_E}{dt} = \frac{dC_P}{dt} + \frac{dC_S}{dt} = -N_E = G_P - R_E, \quad (1)$$

where C_E is the ecosystem carbon density (typically Mg C ha⁻¹ or mol C m⁻²), C_P is the density of the live plant carbon pool, C_S is the density of the soil carbon pool which also includes the dead plant litter pool (including coarse woody debris), and N_E is the rate of net ecosystem exchange, equal to the ecosystem (plant + soil) respiration rate (R_E) less the rate of net CO₂ assimilation through photosynthetic processes, the latter often being referred to as gross primary productivity, G_P , or GPP. The sign of change in carbon density reflects the atmospheric convention, where emissions are positive and a net carbon uptake by vegetation is negative.

The rate of change in plant carbon can be expressed as

$$\frac{dC_P}{dt} = N_P - L_P, \quad (2)$$

where N_P is the net primary productivity (NPP) of the ecosystem (defined as the rate of new plant growth), and L_P represents the losses from the live plant carbon pool, being equivalent to the sum of the rates of litterfall, herbivory, and tree mortality. Likewise for soil carbon

$$\frac{dC_S}{dt} = L_P - R_H, \quad (3)$$

where R_H is the rate of heterotrophic respiration. The equivalences in equation 1 arise because $R_E = R_P + R_H$ with R_P being the rate of autotrophic (plant) respiration and with $N_P = G_P - R_P$. That is to say,

$$\frac{dC_P}{dt} + \frac{dC_S}{dt} = N_P - R_H = G_P - R_P - R_H = G_P - R_E = -N_E. \quad (4)$$

In terms of the different methodologies applied, tower-based eddy covariance measurements attempt to determine stand level carbon balances by measuring N_E continuously over a period of 1 year or more [Saleska *et al.*, this volume]. On the other hand, biomass inventory measurements provide a direct estimate of dC_P/dt or, more precisely, the rate of change in the carbon stocks of aboveground woody biomass between two or more census dates which are typically separated by a period of 5 to 10 years [Phillips *et al.*, this volume]. Thus, any long-term changes in leaf and root carbon stocks, as well as in soil and litter carbon stocks, are not usually taken into account using biomass inventory approaches.

3.2. Tower-Based Eddy Covariance Approach

Grace *et al.* [1995a] used a combination of direct eddy covariance measurement [Grace *et al.*, 1995b, 1996] and modelling approach [Lloyd *et al.*, 1995] to estimate the carbon balance of semievergreen tropical forest in southwest Amazonia, inferring a net carbon sink (dC_E/dt) of about 1.0 Mg ha⁻¹ a⁻¹. Although consistent with what might be theoretically expected if increasing atmospheric [CO₂] were stimulating growth of tropical forest trees [Taylor and Lloyd, 1992; Lloyd and Farquhar, 1996], the suggestion that old growth rain forests should not be steady state systems proved immediately controversial [Keller *et al.*, 1996], with other authors arguing that both short- and long-term disturbance regimes needed to be taken into account [Clark, 2004, 2007; Chambers *et al.*, 2004] (discussed further in section 3.3). Nevertheless, subsequent work by the same group in an evergreen

tropical forest near Manaus suggested an even larger carbon sink of $5.7 \text{ Mg ha}^{-1} \text{ a}^{-1}$ [Malhi *et al.*, 1998], which led Malhi and Grace [2000] to suggest that tropical forests might be sequestering as much as 2.0 Pg C a^{-1} on a global scale, effectively accounting for the bulk of the terrestrial carbon sink. Several subsequent studies above Amazonian forests have also inferred them to be substantial carbon sinks [Carswell *et al.*, 2002; Araújo *et al.*, 2002], although recently disturbed forests may not be [Keller and Crill, 2000; Saleska *et al.*, 2003].

It has become increasingly apparent, however, that the eddy covariance technique yields what seem to be erroneously low estimates of ecosystem carbon dioxide efflux rates on calm nights, even when changes in the amount of CO_2 stored within the canopy space are taken into account [Goulden *et al.*, 1996]. Thus, below a certain turbulence threshold, it is now more or less common practice to substitute observed data with data simulated from a model calibrated with measurements made under conditions of stronger vertical mixing [Loescher *et al.*, 2005]. Nevertheless, estimated annual carbon balances can be drastically altered depending on the apparent turbulence threshold used [Miller *et al.*, 2004]. Thus, accounting for this effect is not straightforward. For example, even though an apparent “flux loss” may be observed on calm nights, it has also been shown that 24-h integrals may be independent of the nighttime turbulence regime [Kruijt *et al.*, 2004]. In such a situation, corrections for nighttime flux losses might, in fact, not be appropriate.

Saleska *et al.* [2003] suggest that nighttime flux losses should always be “corrected” for. Their argument was based, in part, on the observation that correcting for nighttime fluxes caused near-identical net annual ecosystem carbon balances to be calculated for their tower and another approximately 20 km distant. But such logic is at odds with another conclusion of Saleska *et al.* [2003] in that their forest was a significant source of CO_2 to the atmosphere because of CO_2 emissions from the unusually high amounts of coarse woody debris (CWD) at that site. As noted by Rice *et al.* [2004] the site sampled by Saleska *et al.* [2003] contained about 50% more CWD than the site with which they were comparing [Miller *et al.*, 2004]. It can simply be estimated, other things being equal, that this should have caused a difference in overall carbon balances between the two sites of approximately $2 \text{ Mg ha}^{-1} \text{ a}^{-1}$.

Other justifications for applying any given magnitude of nighttime correction to eddy flux measurements are also debatable. For example, Saleska *et al.* [2003] suggested that similar estimates of the carbon balance from eddy covariance measurements and aboveground woody biomass inventory measurements provide another justification. But only

about 0.1 of tropical forest G_P [less than 0.3 of N_P in (2)] ends up being allocated to wood production [Malhi *et al.*, 1998; Saleska *et al.*, 2003; Aragão *et al.*, 2009].

It thus seems to us that there is no single reliable or scientifically defensible diagnostic to indicate the correct magnitude of any “corrections” to be applied under conditions of low turbulence in eddy covariance studies, and we are thus left to conclude that stand level carbon balances estimated by the eddy covariance method, whether quoted as being negative or positive, are not resolved with sufficient accuracy to allow meaningful estimates of dC_E/dt to be made. Daytime CO_2 flux may also be biased because the eddy covariance technique does not usually close the energy budget during daytime [Wilson *et al.*, 2002; Aranibar *et al.*, 2006]. Taken in conjunction with the need to consider other carbon fluxes not measured by the technique, such as those associated with emissions of volatile organic compounds [Kesselmeier *et al.*, this volume], fluxes of dissolved organic (DOC) and inorganic (DIC) carbon into riverine systems through the soil system [Richey *et al.*, this volume], and nocturnal cold air drainage [Goulden *et al.*, 2006; Araújo *et al.*, 2007], the main potential of the eddy covariance technique would seem to lie most in understanding drivers of intra-annual and interannual variability in G_P , R_P , and R_H [e.g., Miranda *et al.*, 1997; Saleska *et al.*, 2003; Vourlitis *et al.*, 2005] and also in the acquisition of data to aid the calibration and development of ecosystem-level gas exchange models [e.g. Lloyd *et al.*, 1995; Mercado *et al.*, 2006; Baker *et al.*, 2008; Mercado *et al.*, 2009].

Even then, the meaningful scaling of any derived parameters to the basin-wide scale must remain problematical, as all eddy covariance towers in Amazonian forest are currently confined to the relatively infertile oxisol and dystrophic ultisol soil types (ferralsols and Acrisols/Alisols in the new World Reference Base soil classification system). These occupy only about 0.65 of the Amazon Basin area, with other soil types, most of which are more fertile, occupying the remaining 0.35 [Quesada *et al.*, 2009]. Although such forests are well studied in terms of aboveground biomass dynamics [Phillips *et al.*, this volume], we currently know nothing about the magnitudes and environmental modulation of rates of their canopy gas exchange. However, it does seem likely that due to significantly higher foliar nutrient concentrations [Fyllas *et al.*, 2009; Lloyd *et al.*, this volume], the photosynthetic properties of these forests should be substantially different from their less fertile eastern and central Amazonian counterparts [Mercado *et al.*, 2009]. As discussed below, forests growing on more fertile soils also seem to be accumulating carbon at a higher rate than forests growing on the less fertile ferralsols and Acrisols/Alisols of central and eastern Amazonia.

3.3. Plot-Based Biomass Approach

Phillips et al. [1998] first reported that Amazonian and other tropical forests appeared to be increasing in above-ground biomass (AGB), a result that has since been expanded upon and refined by *Baker et al.* [2004], the latter study estimating an average rate of increase in the carbon stocks of Amazonian forest to be $1.22 \pm 0.43 \text{ Mg ha}^{-1} \text{ a}^{-1}$. *Baker et al.* [2004] also showed that this increase in biomass was not uniform across the Amazon Basin, but rather seemed to be greatest for forests growing on the more fertile soils of western Amazonia, with rates of AGB accumulation also being especially high for forests growing on Holocene floodplain and contemporary floodplain plots [see also *Phillips et al.*, this volume]. This suggested an overall aboveground carbon sink in the Amazon Basin of $0.6\text{--}0.8 \text{ Pg a}^{-1}$.

Nevertheless, as for eddy covariance measurements, these results have proved controversial, with possible methodological errors and biases having been suggested as giving rise to this apparent AGB increase [*Clark, 2004; Wright, 2005*]. Many of these concerns seem to have been addressed and/or refuted [*Phillips et al., 2002; Baker et al., 2004; Lewis, 2006*], and attention of those philosophically opposed to a tropical forest carbon sink has turned more to the possibility that the permanent plot sampling network does not adequately capture significant carbon losses. This has been suggested to arise either as a consequence of small scale but regular disturbances (such as may occur over areas of order 0.1 to 1.0 ha on a timescale of the order of decades) not being adequately detected by the current network or because current rates of AGB accumulation merely reflect the recovery of forests from significant past disturbances [*Keller et al., 1996; Saleska et al., 2003; Chambers et al., 2004; Wright, 2005; Clark, 2007*]. Examples of possible major events proposed by these “catastrophists” include the great drought of 1926 [*Williams et al., 2005*] or mega-Niño events occurring many centuries ago [*Meggiers, 1994*].

Such arguments are, however, hard to justify on even simple quantitative grounds. For example, as is also acknowledged by *Chambers et al.* [2004], if forests are recovering from some sort of disturbance regime, then rates of new stem growth would be expected to be decreasing with time, as the ecosystem approaches a new equilibrium. But, as has been shown by *Lewis et al.* [2004], for a range of plots across Amazonia, the opposite is, in fact, observed: stem growth rates are continually increasing. Likewise, if rates of AGB accumulation are currently around 0.7 Pg C a^{-1} across the basin [*Baker et al., 2004*], as a result of recovery from some past mega-disturbance such as the 1926 drought [*Guariguata and Ostertag, 2001*], and if they have been accumulating biomass at that rate for 80 years, then the amount of carbon

released from that drought must have been at a minimum 60 Pg C , which would equate to an increase of about $25 \mu\text{mol mol}^{-1}$ in global atmospheric $[\text{CO}_2]$ if it had all remained in the atmosphere. Of course, if such an event had occurred, then much of the carbon released would have been relatively quickly taken up by the oceans, but nevertheless, such a massive release of carbon, even if spread over a decade, would still have remained discernable in the recent Southern Hemisphere ice-core record. No such signal is apparent [*Etheridge et al., 1996*], and thus the notion that many Amazonian forests must be recovering from severe carbon losses as a consequence of the 1926 event is unsubstantiated.

Baker et al. [2004] provide several further lines of argument as to why the observed increase in forest biomass is not just a simple artefact, and analysing the data set in more detail, *Lewis et al.* [2004] also concluded that increased rates of forest growth in response to continually increasing atmospheric $[\text{CO}_2]$ or radiation were the most likely explanation for this AGB increase in Amazonian forests. Those authors also noted that, as for the increase in AGB, tree growth rates seemed to be being stimulated to a greater extent in the more fertile forests of western Amazonia.

Not all studies, whether inside or outside of Amazonia, find increased growth rates. Changes in living wood, including recruitment and mortality as well as growth, was near steady state in Manaus, but accumulating carbon ($\sim 1.5 \text{ Mg C ha}^{-1}$) in Santarém and Rio Branco [*Vieira et al., 2004*]. The authors suggested the accumulations were related to previous disturbances, and similarly, *Fisher et al.* [2008] have recently used an area-based stochastic simulator of forest disturbance and recovery to suggest that current measurements of an increase in AGB in Amazonia may, indeed, just be simple sampling artefacts. Yet the data analysis protocol and some fundamental assumptions implicit in the latter analysis may be flawed [*Lloyd et al., 2009a*], and a more rigorous data-based analysis of results from the Amazon RAINFOR plot network [*Phillips et al., this volume*] has shown that, overall, the reported AGB increase for Amazon forests is almost certainly real [*Gloor et al., 2009*].

Nevertheless, only four out of ten plots (16–52 ha each) sampled throughout the tropics showed a significant increase in aboveground biomass, for a combined average rate of $0.24 \text{ Mg C ha}^{-1} \text{ a}^{-1}$, a value on average lower than reported for Amazonia; this being attributed to either an increase in resource availability (presumably light and/or CO_2) or a recovery from past disturbance [*Chave et al., 2008*]. Interestingly, the latter explanation was based, at least in part, on increased growth rates being higher (in relative terms) for slower growing late succession species. Yet it is quite possible that slower growing species with high respiratory requirements might respond proportionally more to increases in CO_2 than

faster growing ones [Lloyd and Farquhar, 1996, 2000], and it is also the case that late successional species growing under light-limited conditions should be more responsive to increases in CO₂ than larger trees exposed to higher light levels higher up in the canopy stratum [Lloyd and Farquhar, 2008]. Thus, it is not necessary to include disturbance-based recovery as an explanation for the results of Chave *et al.* [2008], as they are, in fact, consistent with what we might expect for an ecosystem level stimulation of growth by increasing [CO₂]. Two of the large plots (50 ha) examined by Chave *et al.* [2008], one in Panama and one in Malaysia, were also reported to show declining rates of tree growth [Feeley *et al.*, 2007]. The changes in growth were related to regional climate changes: minimum daily temperature, precipitation, and insolation, with increased carbon losses associated with higher respiration rates at warm temperatures in recent years being considered the most likely explanation. It has, however, been shown by Lloyd and Farquhar [2008] that, if higher plant respiration rates were accounting for the decline in growth observed by Feeley *et al.* [2007], the Q_{10} for autotrophic respiration would be unreasonably high. They suggested that stomatal closure in response to higher canopy-to-air vapor pressure deficits in dry years was a more likely explanation. For the Pasoh forest in Malaysia, at least, ongoing soil acidification as a consequence of increasingly high rates of nitrogen- and sulfur-based pollutants in the region [Lewis *et al.*, 2004] is another potential cause.

One interesting question is the extent to which the currently increasing AGB of Amazonian forests is associated with changes in other carbon pools. That is, the results of Baker *et al.* [2004] reflect only one component of the dC_p/dt term in (1); with leaf and root biomass changes not considered. Moreover, aboveground coarse woody debris (CWD) and the dC_s/dt term are totally ignored. It is unlikely that significant changes in leaf biomass are currently occurring for tropical forests because their leaf area indices (LAI) are already very high [Lloyd and Farquhar, 1996]. The short turnover time for leaves argues against any significant long-term accumulation of carbon [Lloyd and Farquhar, 1996]. This should also be the case for fine roots [Lloyd, 1999], for which overall biomass in Amazonian forests is, in any case, rather small [Aragão *et al.*, 2009]. Based on the data available [Cairns *et al.*, 1997; Mokany *et al.*, 2006], however, it does seem likely that belowground coarse (woody root) carbon stocks should be increasing at about 0.25 the rate of increase in AGB, i.e., around 0.3 Mg C ha⁻¹ a⁻¹ or 0.2 Pg C a⁻¹ on a basin-wide basis.

On the other hand, aboveground CWD may not follow changes in AGB. In a forest near Santarém, Pará, CWD was recently observed to decline, while AGB was increasing [Pyle *et al.*, 2008]. The observation was believed to result

from a recent disturbance, which transferred a fraction of AGB to CWD. The net flux of carbon at the site was a source to the atmosphere, despite increasing AGB, and the net source was expected to last 10–15 years before the annual uptake of carbon in recovering AGB exceeded the annual loss in decaying CWD. The net source of carbon from the ecosystem despite a net accumulation in AGB calls attention to the importance of full carbon accounting.

If carbon is accumulating in AGB, it may also be accumulating in the soil carbon pool [the dC_s/dt term in (1)] as the extra live carbon accumulating aboveground and belowground must eventually be transferred to the litter and humus pools [Lloyd and Farquhar, 1996]. From theoretical principles we know that the magnitude of this accumulation should be dependent on both the rate at which plant litterfall and mortality increases in response to stimulated growth, itself dependent on dC_p/dt , as well as the complex spectrum of litter and soil carbon turnover times [Lloyd, 1999]. A short turnover time for litter, for example, would preclude any significant long-term accumulation of carbon.

Available data on the different soil carbon pools and their associated turnover times are rare, but Telles *et al.* [2003] used radiocarbon isotope analysis to calibrate a simple model of soil carbon dynamics for some relatively infertile ferrasol and Acrisol soils of central and eastern Amazonia. They concluded that associated with a rate of increase in AGB of ~0.5 Mg C ha⁻¹ a⁻¹ should be an accumulation of carbon in soil of about 0.2 Mg C ha⁻¹ a⁻¹, yet they observed no measurable change in organic carbon stocks over the past 20 years. Their simulated rate should be higher for the more fertile forests of western Amazonia, where AGB is accumulating carbon at a faster rate [Baker *et al.*, 2004]. A second important factor contributing to greater rates of carbon accumulation in the more fertile soils of the western portion of the basin may be the characteristic differences in clay mineralogy between the ferrasols/Acrisols of central and eastern Amazonia and the Cambisols and other more fertile soil types of the western portion of the basin. Most of the former are dominated by kaolinite [Irion, 1984], including the actual sites sampled by Telles *et al.* [2003]. On the other hand, reflecting a different parent material as well as different weathering conditions (typically less well drained), the soils of western Amazonia are typically dominated by 2:1 clays [Irion, 1984; Quesada *et al.*, 2009], which are characterized by stronger mineral-organic matter associations and hence longer mean residence times for soil carbon [Wattel-Koekkeok *et al.*, 2003]. This means that, relative to the rate of AGB accumulation, substantially more carbon may, in fact, be accumulating in these western Amazonian soils, especially when it is also considered that many of these soils are still weathering and contain considerable amounts of noncrystalline secondary iron and

aluminum oxide minerals (Lloyd and Quesada, unpublished data). The latter bond more extensively to soil organic matter than the more crystalline forms, such as hematite and kaolinite [Torn *et al.*, 1997]. The carbon dynamics of the soils of the Amazon Basin are discussed in more detail by Trumbore *et al.* [this volume].

4. CARBON BALANCE OF AQUATIC SYSTEMS

The streams, rivers, and wetlands of Amazonia appear to be net sources of carbon, releasing an estimated 0.5 Pg C a^{-1} to the atmosphere [Richey *et al.*, 2002, this volume]. If this efflux were attributable to a displaced respiration from terra firma forests, it would offset some of the annual net sinks of CO_2 measured by eddy covariance at tower sites. But it is unclear what fraction of terra firma forest NPP (or what fraction of upland areas) is contributing to this aquatic respiration. It has generally been supposed that the productivity of seasonally flooded forests should be relatively high due to their occurrence on generally fertile alluvial soils [Worbes, 1997; Parolin *et al.*, 2004], and this seems to be the case for várzea (seasonally flooded white water forests), which are among the most productive in the Amazon Basin [Malhi *et al.*, 2004]. Nevertheless, it would seem likely that igapó (seasonally flooded black or clear water forests) have a lower productivity than várzea due to the overall lower nutrient levels of their supporting soils [Quesada *et al.*, 2009]. Indeed, Worbes [1997] reported significantly higher litterfall rates for várzea than igapó. The ratio of fine litterfall to aboveground (stem) growth rates for várzea (about 1.6) was similar to that observed for Amazon terre firme forests [Aragão *et al.*, 2009], with most leaf litterfall occurring during the flooding period [Worbes, 1997; Parolin *et al.*, 2004] and thus directly into the aquatic system.

From the above observations, a reasonable estimate for leaf litterfall input to rivers from seasonally flooded forests is $5 \text{ Mg C ha}^{-1} \text{ a}^{-1}$, allowing calculation of the total (Amazon basin-wide) river input from seasonally flooded forest foliar litterfall as follows: Seasonally flooded areas for a study site of $1.8 \times 10^6 \text{ km}^2$ in the central Amazon Basin [Hess *et al.*, 2003] and a $2.2 \times 10^6 \text{ km}^2$ area of western Amazonia [Toivonen *et al.*, 2007] accounted for about 0.17 of the areas. Assuming the fraction of seasonally flooded areas occupied by forests is ~ 0.7 [Hess *et al.*, 2003] implies a total area of seasonally flooded forest in the Amazon Basin of $0.48 \times 10^6 \text{ km}^2$ or $4.8 \times 10^7 \text{ ha}$. Multiplying this by the estimated leaf litterfall rate of $5 \text{ Mg C ha}^{-1} \text{ a}^{-1}$ gives a net direct input of $\sim 0.25 \text{ Pg C a}^{-1}$ into the Amazon river system, almost all of which would be expected to be respired downriver and thus part of the Richey *et al.* [2002] measured efflux of approximately 0.5 Pg C a^{-1} .

Though occupying only about 0.1 the area of seasonally flooded forest, C_4 aquatic grasses are a second potentially significant autochthonous source into the Amazon river system. The NPP of these grasses is very high, estimated to be of the order $50 \text{ Mg C ha}^{-1} \text{ a}^{-1}$ [Piedade *et al.*, 1991], yet ecosystem respiration rates from such wetlands are low [Morison *et al.*, 2000], suggesting that much of the carbon assimilated by aquatic grasses must be transported to, and respired in, the main river system, estimated from the above numbers as $\sim 0.25 \text{ Pg C a}^{-1}$. These estimates, combined with observations that the rates of loss of dissolved organic carbon [Waterloo *et al.*, 2006] and dissolved CO_2 [Davidson *et al.*, 2008] from terre firme forests to rivers are low, suggest that inputs into the Amazon river system from seasonally flooded forests and aquatic grasses may well be sufficient to account for the 0.5 Pg C a^{-1} net efflux observed by Richey *et al.* [2002]. This explanation is consistent with the very young age of the carbon respired from the Amazon River system and with a ^{13}C isotopic composition indicative of a C_4 source [Mayorga *et al.*, 2005]. It is also consistent with the review by Melack *et al.* [this volume] that flooded forests and aquatic macrophytes account for 96% of the carbon inputs to the river.

It is possible that the efflux of carbon from wetlands is only a fraction of the inputs from terrestrial systems (that the aquatic sediments are a net carbon sink). We know that little carbon is exported by the Amazon River to the ocean (0.07 Pg C a^{-1}) [Richey *et al.*, 1990], but of the inputs to aquatic systems (both allochthonous and autochthonous), the fractions respired, as opposed to accumulating, are unknown. In two watersheds in the United States, erosion and deposition were estimated to yield a net sink of the order of 1% of NPP [Berhe *et al.*, 2007]. If the same fraction of NPP is sequestered in Amazonia, the sink would be on the order of 0.1 Pg C a^{-1} (NPP is approximately 10 Pg C a^{-1}) [Potter *et al.*, 2004] (see section 5).

It thus seems that the role of wetlands and rivers in the regional carbon balance is nearly neutral, with the aquatic efflux of 0.5 Pg C a^{-1} balanced by autochthonous inputs from seasonally flooded forests and grasslands.

5. CARBON BALANCE OF AMAZONIAN REGIONS: ECOSYSTEM MODELS BASED ON PHYSIOLOGY

Ecosystem carbon models have been used to estimate Amazonia-wide fluxes of carbon by scaling up measurements and processes observed at fine scales. Not surprisingly, both the models themselves and the estimates they provide vary. Furthermore, models have been used to address different components of the carbon balance. The distinction pertinent for this discussion is between those modeling studies

that have focused on the physiological processes governing natural fluxes of carbon and those that have focused on disturbance and recovery processes, both anthropogenic and natural. The two types of studies are reviewed in this and the next section, respectively. Sometimes the same model has been used to address both types of processes.

Terrestrial biogeochemical models have been used to calculate the fluxes of carbon from photosynthesis (GPP), NPP, and heterotrophic respiration (R_H), including decay. To one degree or another, all of the models reviewed here attempt to compute rates of plant carbon uptake and litter decomposition as influenced by environmental variables (radiation, temperature, precipitation, and nutrients). In some models, NPP is driven with environmental data alone; in others, it is determined by changes in leaf-area index, inferred from NOAA's advanced very high resolution radiometer (AVHRR) satellite or NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) satellite [Potter *et al.*, 1999].

Several studies have examined how interannual variations in climate affect the carbon balance of the Amazon Basin [Kindermann *et al.*, 1996; Tian *et al.*, 1998; Prentice and Lloyd, 1998; Asner *et al.*, 2000; Potter *et al.*, 2001a, 2001b, 2001c; Foley *et al.*, 2002]. All of the studies found that the net annual flux of carbon is significantly correlated with ENSO events. The Amazon Basin appears to be a significant carbon source during El Niño events and a sink during La Niña events, consistent with atmospheric inverse calculations (section 2.1) (Figure 1). Model estimates of the El Niño source varied from 0.17 to 0.4 Pg C a⁻¹; estimates of the La Niña sink varied from -0.27 to -0.7 Pg C a⁻¹ [Tian *et al.*, 1998; Potter *et al.*, 2001a, 2001b, 2001c, 2004; Foley *et al.*, 2002]. Most of these studies concluded that the major variations in regional carbon balance are related chiefly to changes in precipitation.

Foley *et al.* [2002], using Integrated Biosphere Simulator (IBIS) [Foley *et al.*, 1996; Kucharik *et al.*, 2000], found that changes in carbon balance are largely driven by changes in ecosystem productivity, linked to changes in soil moisture and drought stress. Potter *et al.* [2001a, 2001b, 2001c] also found that drought during El Niño years reduced NPP. Periods of relatively high solar surface irradiance combined with several months of adequate rainfall were required to sustain the forest carbon sink.

Notwithstanding the observation that TEM [Melillo *et al.*, 1993; McGuire *et al.*, 1995, 2001; Tian *et al.*, 1998], NASA-CASA [Potter *et al.*, 2001a, 2001b, 2001c, 2004], and IBIS [Foley *et al.*, 1996; Kucharik *et al.*, 2000] all reproduced net annual sources of carbon during El Niño years and net annual sinks during La Niña years, they did a poor job reproducing seasonal carbon fluxes for the tropical evergreen forests near Santarém, Pará, Brazil [Saleska *et al.*, 2003]. Photosynthesis

is apparently less water stressed, seasonally, than the models predict and more light limited. The trees are able to acquire water from deep roots [Nepstad *et al.*, 1994] or by hydraulic redistribution of soil water [Rocha *et al.*, 2004; Oliveira *et al.*, 2004]. Heterotrophic respiration in the upper soil layers, on the other hand, probably is limited by soil water. Thus, reduced respiration contributes to the greater net uptake of carbon during dry seasons [see Saleska *et al.*, this volume] for a more detailed discussion of seasonality, including apparent differences in the water stress of vegetation in different parts of Amazonia).

The fact that ecosystem models failed to reproduce even the sign of the seasonal fluxes of carbon raises the question of whether they simulate accurately year-to-year variations in flux. The recent observation that Amazonian forests may have greater photosynthesis during the dry season than the wet season is also the reverse of what most models simulate [Saleska *et al.*, 2007]. It has recently been shown, however, that the simultaneous inclusion of water storage to large depth, the ability of roots to extract water from such depths as the surface soil dries, an allowance for hydraulic redistribution to occur allowing for more efficient water uptake during the wet season and moistening of the near-surface soil during drought, and the inclusion of a photosynthetic response to high light levels during the dry season, including all of these processes in model simulations, does allow such observations to be simulated [Baker *et al.*, 2008]. An analysis of the physiological mechanisms responsible in the models for variations in metabolism seems vital but is beyond the scope of this review.

Although NPP in the humid tropics has been observed to increase during the dry season [Saleska *et al.*, 2003; Huete *et al.*, 2006], it is unlikely that an extended drought would lead to an increased storage of carbon. For example, ENSO events seem to be associated with reduced sinks or larger sources of carbon. Nevertheless, it is unclear whether the larger sources during ENSO are physiological (differential changes in photosynthesis and respiration) or disturbance-based (fires).

The relative importance of water, as opposed to light, in limiting photosynthesis is complicated by the effects of aerosols, which are at higher concentrations during the dry season as a result of fires. Aerosol loading increases photosynthesis initially because it increases diffuse radiation. At higher loadings, however, the lower total radiation reduces photosynthesis more than the diffuse radiation increases it [Oliveira *et al.*, 2007].

It seems likely that short-term responses to drought (or increased radiation) are opposite to long-term responses. During protracted droughts, vegetation may eventually become water stressed [Nepstad *et al.*, 2007; Brando *et al.*,

2008]. In a simulation with IBIS, *Botta et al.* [2002] found that the Amazon Basin can have long-term, climate-induced variations in carbon balance. Considering only variations in climate (and not in CO₂ or land use), they found that Amazonia was almost neutral from the late 1930s to the late 1950s (−0.42 Pg C over 1935–1957), a net carbon source during the 1960s (+1.98 Pg C over 1958–1967), a net sink during the 1970s (−2.54 Pg C over 1968–1978), and back to nearly neutral during the 1980s and 1990s (+0.61 Pg C over 1979–1995).

The recent neutral trend is not obtained with other analyses. Over the 18-year period 1982–1999, both the NASA-Carnegie-Ames-Stanford approach (CASA) model [*Potter et al.*, 2004] and global biome model-biogeochemical cycle (BIOME-BGC) [*Nemani et al.*, 2003] predicted an increase in NPP. The long-term observation that cloudiness has decreased (net radiation increased) over this period led both models to calculate an increase in NPP, in the case of [*Nemani et al.*, 2003] an increase in Amazonian NPP that accounted for 42% of the global NPP increase. That trend in radiation has recently been questioned, however [*Evan et al.*, 2007]. The long-term trend in cloudiness may be an artifact of the satellite record.

Rates of disturbance, both anthropogenic and natural, may be as important as climate variability in affecting ecosystem composition and carbon dynamics in the Amazon region [*Botta and Foley*, 2002]. Using IBIS to examine the effects of climate variability (using either long-term average climate or actual historical variations in climate) and ecological disturbances, *Botta and Foley* [2002] found that interannual climate variability and frequent disturbances both favor grasses over trees, causing large increases in the geographic extent of savanna in the south and east of the region. A more constant climate and less frequent disturbances both favor trees over grasses, causing forest to dominate most of the study area.

Similar results, suggesting that changes in land use may lead to changes in regional climate with consequences for carbon storage, have been obtained with atmospheric general circulation models [*Cox et al.*, 2000; *Betts et al.*, 2004]. *Oyama and Nobre* [2003] showed, for example, that the loss of Amazonian forests could change the existing climate-vegetation system to a drier equilibrium state, with savannization in parts of Amazonia and desertification in the driest area of Northeast Brazil. The conversion of forests to degraded pasture and soybean croplands increased surface air temperatures and decreased evapotranspiration and precipitation, especially in eastern Amazonia [*Sampaio et al.*, 2007]. The continued expansion of cropland in Amazonia could have important consequences for the continued existence of the region's forests and, hence, for carbon storage [*Nepstad et al.*, 2008].

6. SOURCES AND SINKS OF CARBON FROM LAND USE CHANGE, DISTURBANCE, AND RECOVERY

Several analyses have calculated the net emissions of carbon from Brazilian Amazonia as a result of land use change, management, and disturbance. All of the analyses have considered deforestation and regrowth of secondary forests within the moist forest zone. They differ with respect to whether they considered changes in soil carbon, whether they included cerrado, and whether they considered timber harvest, fires, or other disturbances. Even if all of these processes were included, it is important to recognize that the net flux attributable to disturbances is not necessarily the total net flux of carbon for the region. Nor is it equivalent to the fluxes estimated from the biogeochemical models discussed in section 5. The analyses discussed in this section do not include the fluxes in undisturbed ecosystems.

All of the analyses calculate a net carbon source within the range of 0.15 to 0.35 Pg C a^{−1} [*Fearnside*, 1997; *Houghton et al.*, 2000; *Potter et al.*, 2001c; *DeFries et al.*, 2002; *Hirsch et al.*, 2004; *Ramankutty et al.*, 2007]. Uncertainties in biomass, deforestation rate, and rates of decomposition were estimated to account for 60%, 25%, and 15% of the uncertainty in flux estimates [*Houghton et al.*, 2000], and thus, the higher estimates were largely the result of higher estimates of biomass [*Hirsch et al.*, 2004; *Ramankutty et al.*, 2007]. The relatively small error from deforestation rate is unique to this region of the tropics. Annual rates of deforestation in Brazilian Amazonia are better documented than elsewhere. For all of Brazil, *DeFries et al.* [2002] estimated higher average emissions for the 1990s (0.28 Pg C a^{−1}) than for the 1980s (0.15 Pg C a^{−1}). Most of the net flux was attributable to burning and decay of vegetation and slash, with only a small uptake by secondary (regrowing) forests. Sources or sinks of carbon in soils were ignored in these studies, as were logging and fire.

Adding fires [see *Longo et al.*, this volume], *Potter et al.* [2001c] used a version of the NASA-CASA model, together with Landsat-derived mapping of burned areas for the Legal Amazon [*Alves*, 1999], to estimate total fluxes of 0.2 to 1.2 Pg C a^{−1} for the entire Legal Amazon. The variation depended strongly on annual rainfall patterns. Based on an analysis of fire counts during 1992–1993, *Potter et al.* [2001c] calculated a net flux of 0.77 Pg C a^{−1}, of which 0.71 Pg C a^{−1} was from fires and only 0.056 Pg C a^{−1} was from postburning (decomposition). Furthermore, 75% of the fires were in the cerrado, outside of the moist forest area included in other studies. In comparison, *Van der Werf et al.* [2003] used the CASA model with inputs of rainfall from the NASA Tropical Rainfall Monitoring Mission to calculate annual carbon emissions from fires in the Legal Amazon of 0.2 to 0.5 Pg C a^{−1}.

Adding logging [see *Asner et al.*, this volume] to the analysis increased estimates of the net emissions of carbon. *Asner et al.* [2005] calculated a gross source of 0.08 Pg C a^{-1} from decomposition of roundwood, residual stumps, branches, foliage, and roots left on site following wood harvest. The value is a gross flux because logged forests will presumably accumulate carbon as they regrow. However, many logged forests are not permitted to regrow. Approximately a third of the logged forests are cleared for agriculture before they recover [*Asner et al.*, 2006]. The probability that logged forests will be cleared is four times greater than the probability that unlogged forests will be cleared. The finding is consistent with another study of the region, which found that the mean age of secondary forests (4.4 to 4.8 years) had changed very little between 1978 and 2002 [*Neeff et al.*, 2006]. The average age did not increase because secondary forests were usually re-cleared.

Adding soils [*Trumbore et al.*, this volume] to the analysis also increased the emissions of carbon as a consequence of cultivation. Most of the lands deforested in Amazonia are not cultivated, however, but used for pasture. *Cerri et al.* [2007] report that the conversion of forest to well-managed pastures causes an initial decline in soil carbon stocks (0–20 cm) followed by a slow rise to levels exceeding those under native forest. In degraded pastures, the carbon stocks may not recover.

New data and analyses from LBA suggest that the next generation of emission estimates from land use change and management are likely to have smaller errors. For example, two new estimates of forest biomass at high spatial resolution [*Malhi et al.*, 2006; *Saatchi et al.*, 2007; *Phillips et al.*, this volume] and more detailed accounting for differences in wood density and allometric equations [*Nogueira et al.*, 2008]

should allow more precise estimates of carbon emissions from deforestation. As mentioned above, uncertain estimates of biomass contributed more than any other factor to the variability of flux estimates [*Houghton et al.*, 2000, 2001].

Deforestation for new types of land use [*Morton et al.*, 2006; *Alves et al.*, this volume; *Walker et al.*, this volume] may also affect the emissions of carbon. A greater proportion of deforestation in Mato Grosso in recent years, for example, has been for soybean production rather than for pastures. This change in land use has at least two effects. One effect is to release more carbon more rapidly. Aboveground biomass and woody roots are removed rapidly and completely when the land is cultivated, as opposed to grazed. Cultivation leaves little forest biomass for decomposition and delayed emissions. Second, cultivation leads to a 25–30% loss of soil organic carbon from the top meter.

7. SYNTHESIS: WHAT DO WE KNOW?

The net flux of carbon between Amazonia and the atmosphere is small relative to the stocks of carbon held in the vegetation and soils of the region's forests and small relative to the background, or natural, fluxes of carbon annually taken up and released through photosynthesis and respiration. Thus, determining the net flux is difficult. As a result, at least five different approaches have been used to estimate this flux or portions of it:

1. Inverse methods based on atmospheric CO_2 and transport are not well constrained because atmospheric transport is poorly known, and CO_2 sampling stations are too sparse. Furthermore, the approach provides limited information on the mechanisms involved or the long-term response to changes in climate.

Table 2. Different Approaches Used to Estimate the Net Sources and Sinks of Carbon for the Amazonian Region^a

	Flux (Mg C ha ⁻¹ a ⁻¹)	Flux (Pg C a ⁻¹)	Chapter Section
Inverse methods		-1.0 to +4.2 ^b	2.1
Vertical profiles		Insufficient data available	2.2
Eddy covariance	Credible range	Insufficient data available	3.2
Permanent plots	-1.2	-0.6 to -0.8	3.3
Aquatic systems	1.2 ± 0.3	0.0	4
Process models		-0.6 to 0.2	5
Disturbance/recovery		0.1 to 0.5	6
Fire		0.1 to 0.3	6
Total ^c		-0.6 to +0.2	

^aNegative values represent a terrestrial sink.

^bAll tropics. If the net carbon balance for Amazonia were in proportion to forest area, the range for Amazonia would be -0.3 to +1.4 Pg C a⁻¹.

^cRange of the values (in italics) that, together, include all ecosystems and all processes.

2. Direct measurements of CO₂ flux at landscape level (eddy covariance) help elucidate the mechanisms important in short-term, metabolic fluxes of carbon but are difficult to extrapolate to the entire Amazonian region.

3. Direct measurement of changes in carbon stocks (inventories) over years capture the longer-term changes but are difficult to attribute to particular mechanisms. The most likely explanation for an increase seems to be that resources have become more available for plant growth (e.g., solar radiation, atmospheric CO₂ concentrations).

4. Ecosystem models, together with eddy covariance measurements, are good for predicting ecosystem responses to short-term variations in climatic factors, but whether they capture the important long-term responses is unclear. Furthermore, early versions of these models did not reproduce observed short-term (seasonal) changes in NPP and heterotrophic respiration.

5. Disturbance, recovery, management, and changes in land use involve large changes in carbon stocks per unit area that are reasonably well known, but the carbon stocks of the forests actually deforested are still uncertain, as is the change in soil carbon stocks in response to grazing.

Only two of these approaches (3 and 5) yield unambiguous information on the sources and sinks of carbon for the Amazonian region (Table 2). Changes in biomass on permanent plots in old-growth forests suggest that these forests have been accumulating carbon over the last ~20 years at a rate of approximately 0.6 to 0.8 Pg C a⁻¹. Changes in land use, management, and fire, on the other hand, release carbon at rates of 0.2 to 0.8 Pg C a⁻¹. Year-to-year variations are large, so that terrestrial ecosystems in Amazonia appear to be a net carbon sink in some years and a net carbon source in others. The data are too uncertain and too variable to specify whether the region has been a net sink or source over the last decade, a conclusion similar to earlier summaries [Davidson and Artaxo, 2004; Ometto *et al.*, 2005].

If the efflux of carbon from rivers includes part of the ecosystem respiration from forests, this efflux is implicitly included in process-based models and, thus, included in the modeled estimates of net carbon balance for intact ecosystems. But it is not included in either of the approaches that yield unambiguous estimates and, therefore, must be added to those estimates for determining a basin-wide estimate of carbon balance. Estimates of carbon inputs from seasonally flooded forests and grasslands suggest, however, that the efflux is largely balanced by autochthonous inputs. Carbon may be accumulating in aquatic sediments, but the magnitude of such an accumulation is not quantified. Thus, including rivers does not change the conclusion that the Amazonian carbon balance is neutral within the errors of measurement.

Summing the carbon sink in old-growth forests (–0.6 to –0.8 Pg C a⁻¹) with the sources from disturbed lands (0.2 to 0.8 Pg C a⁻¹) yields a net flux for the entire region of –0.6 to 0.2 Pg C a⁻¹. Amazonia is essentially balanced with respect to carbon. The causes of the offsetting sources and sinks of carbon are not entirely clear. Rates of deforestation have been greater than rates of reforestation and afforestation, and thus, the net flux of carbon from anthropogenic disturbance and recovery is clearly a net source of carbon to the atmosphere. The accumulation of biomass on permanent plots within old-growth forests, on the other hand, may be the result of a growth enhancement brought about by increased radiation or higher concentrations of CO₂, that is, by physiological responses to changes in the environment. Recovery, rather than metabolic, processes cannot be ruled out, however, because local disturbances are common. The frequency of such natural disturbances is not well quantified but is of critical importance because changes in coarse woody debris as a result of disturbance may offset the accumulations of carbon in aboveground biomass. If such offsets are the rule, the net flux of carbon in old-growth forests would be nearly zero, and the net flux for the region would be a source.

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