Global Change Biology (2005) **11,** 945–958, doi: 10.1111/j.1365-2486.2005.00955.x

Aboveground Forest Biomass and the Global Carbon Balance

R. A. HOUGHTON

Woods Hole Research Center, PO Box 296, Woods Hole, MA, 02543, USA

Abstract

The long-term net flux of carbon between terrestrial ecosystems and the atmosphere has been dominated by two factors: changes in the area of forests and per hectare changes in forest biomass resulting from management and regrowth. While these factors are reasonably well documented in countries of the northern mid-latitudes as a result of systematic forest inventories, they are uncertain in the tropics. Recent estimates of carbon emissions from tropical deforestation have focused on the uncertainty in rates of deforestation. By using the same data for biomass, however, these studies have underestimated the total uncertainty of tropical emissions and may have biased the estimates. In particular, regional and country-specific estimates of forest biomass reported by three successive assessments of tropical forest resources by the FAO indicate systematic changes in biomass that have not been taken into account in recent estimates of tropical carbon emissions. The 'changes' more likely represent improved information than real on-the-ground changes in carbon storage. In either case, however, the data have a significant effect on current estimates of carbon emissions from the tropics and, hence, on understanding the global carbon balance.

Keywords: biomass, carbon sink, deforestation, global carbon, land use, terrestrial carbon

Received 22 September 2004; received in revised form and accepted 23 November 2004

Introduction

The largest errors in estimates of the terrestrial carbon balance are believed to result from uncertain rates of tropical deforestation. However, three recent estimates of carbon emissions from tropical deforestation (Achard *et al*., 2002; DeFries *et al*., 2002; Houghton, 2003) varied only in their rates of deforestation. They used nearly identical data for carbon stocks. Because the carbon stocks of tropical forests are also uncertain (Houghton *et al*., 2001; Eva *et al*., 2003; Fearnside & Laurance, 2003), the range of possible emissions of carbon from tropical deforestation and degradation is broader than commonly thought. For the tropics, uncertainties in biomass may contribute as much to variable estimates of carbon emissions as uncertainties in deforestation rates.

Outside the tropics, the carbon stocks in aboveground forest biomass are reasonably well known as a result of continuous forest inventories (Goodale *et al*., 2002). Despite the high precision of such inventories, however, they are designed to yield *average* wood volumes for administrative units; they do not provide maps of biomass at a resolution compatible with land-use change. If the forests cleared, logged, or burned are systematically different in biomass from 'average' forests, the use of average values will bias the calculated sources and sinks of carbon.

The purpose of this paper is to evaluate the uncertainty of biomass in affecting estimates of terrestrial carbon flux. The paper begins with a description of why biomass is important for the global carbon cycle, turns to an evaluation of how well biomass is known at present, and then discusses how our understanding of the carbon cycle would be enhanced if forest biomass were monitored at a fine spatial resolution (25–250 m), globally.

Direct measurement of biomass on the ground is time consuming (expensive), and repeated measurements, if they occur at all, are generally limited to 10-year intervals. The possibility that aboveground forest biomass might be determined from space is a promising alternative to ground-based methods (Hese *et al*., 2005). Existing space-borne sensors (optical and radar-based) have been used to separate successional stages of forest regrowth (e.g., Steininger, 1996; Rignot *et al*., 1997), but have limited success at determining biomass

Correspondence: R. A. Houghton, e-mail: rhoughton@whrc.org

in closed canopies and in high-biomass forests (Waring *et al.*, 1995). On the other hand, recent airborne investigations with long-wavelength radar and lidar have demonstrated an ability to determine aboveground biomass in temperate zone (Lefsky *et al.*, 1999; Patenaude *et al.*, 2004; Treuhaft *et al.*, 2004) and tropical forests (Drake *et al.*, 2003) and suggest that future satellites could do the same (Lucas *et al.*, 2004; Hese *et al.*, 2005). The purpose of this paper is not to review the capability of different remote-sensing systems, however, but to evaluate the improved understanding of the global carbon balance that would be obtained if forest biomass were determined from space.

Why is the spatial distribution of biomass important in understanding the carbon cycle?

Knowing the spatial distribution of forest biomass is important for at least two reasons. First, a knowledge of biomass is required for calculating the sources (and sinks) of carbon that result from converting a forest to cleared land (and vice versa). While average biomass values have been used in most calculations of carbon flux to date, the possibility that deforestation occurs in forests with biomass that is significantly different from the average suggests that linking specific locations of disturbance with geographically specific estimates of biomass would improve estimates of flux. What is the biomass of the forests actually deforested? A second reason to know the spatial distribution of biomass is to enable measurement of change through time. This reason will be returned to below.

The need to link estimates of biomass to the areas actually disturbed results from the approach generally used to calculate net fluxes of carbon over large areas. The approach is based on (1) changes in forest area (as caused, for example, by changes in land use) and (2) per hectare changes in carbon stocks, also as a result of a change in land use (that is, the carbon stocks before and after land-use change). Figure 1a shows the per hectare changes in carbon that might follow clear-cutting of a northern hardwood forest. Living aboveground biomass is reduced from 70 to 10 Mg C ha^{-1} and subsequently begins to regrow. After about 40 years, in this example, living aboveground biomass has recovered to its preharvest value. The combined pools of dead biomass, belowground biomass, coarse woody debris, and soil organic carbon increase at harvest as a result of slash, stumps, and roots left on site. In the years following harvest, the carbon in these pools declines (decomposes) and then accumulates, again, as the forest ages. Wood products, removed from the forest at harvest, also decline over time. The sum of all of these changes on land results in an immediate release of carbon to the atmosphere in the year of harvest (about 30 Mg C ha^{-1} in this example), a further, smaller annual release over the next ~5 years before the regrowing forest becomes an annual carbon sink, gradually diminishing as the forest matures (Fig. 1b). The carbon released in the first 5 years is balanced by the uptake of carbon in the next ~30 years in this example, but forests may continue to accumulate carbon for centuries.

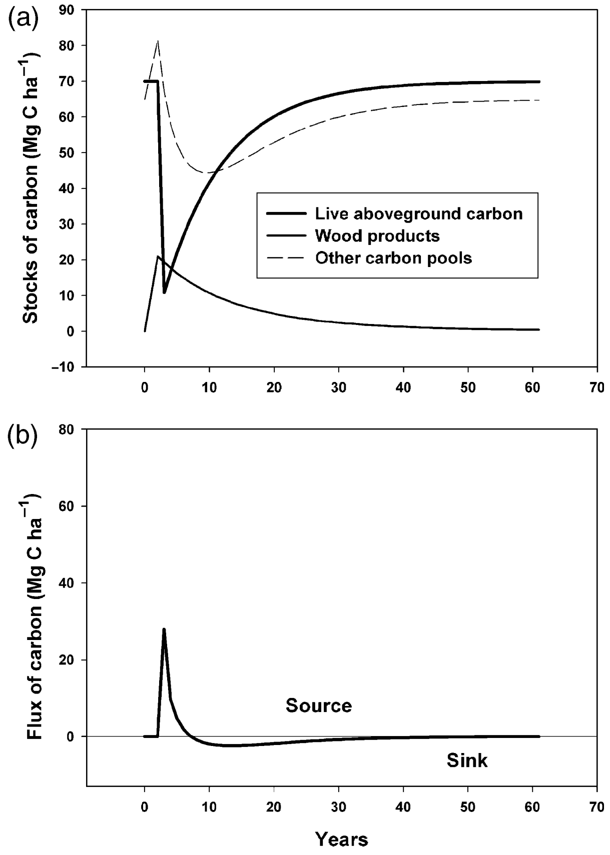

Fig. 1 (a) Idealized changes in living biomass, wood products, and other components of the ecosystem (dead biomass, belowground biomass, coarse woody debris, and soil organic carbon) as a result of harvest and regrowth in a temperate-zone forest. (b) Annual net exchanges of carbon between 1 ha of logged forest and the atmosphere (positive values indicate a source of carbon to the atmosphere).

In many instances, the carbon stocks in forests may change without a change in forest area. Examples include losses of biomass associated with selective wood harvest, forest fragmentation, ground fires, shifting cultivation, browsing, and grazing (e.g., Laurance *et al.*, 1998; Nepstad *et al.*, 1999; Laurance *et al.*, 2000; Barlow *et al.*, 2003), and accumulations of biomass in growing and recovering (or secondary) forests. These changes in biomass are generally more difficult to detect with satellite data than changes in forest area and more difficult to document from census data; yet, the changes in carbon may be significant. Estimates of carbon emissions from the degradation of forests (expressed as a percentage of the emissions from deforestation) range from 5% for the world's humid tropics (Achard *et al*., 2004) to 25–42% for tropical Asia (Flint & Richards, 1994; Iverson *et al*., 1994; Houghton & Hackler, 1999) to 132% for tropical Africa (Gaston *et al*., 1998). In this latter estimate, the loss of carbon from forest degradation was larger than from deforestation. The variation among estimates results, in large part, from the lack of spatially specific data on biomass and the difficulty of identifying and measuring changes in biomass.

The per hectare changes in carbon stocks resulting from changes in forest area (deforestation, reforestation, afforestation) are more easily documented than other changes in carbon stocks for two reasons. First, the changes are large (the biomass of forests is 20–50 times greater than the biomass of agricultural lands), and, second, optical satellite data can detect changes in forest area more accurately than they can infer more subtle shifts in carbon stocks, especially after canopy closure. The good news is that the largest fluxes of carbon are those most easily documented. The not so good news is that estimates of carbon flux are sensitive to rates of deforestation and to the carbon stocks of the forests cleared. Errors in either of these variables will affect the calculated flux.

How well do we know the biomass of the world's forests?

The discussion starts with the simplifying assumption that the changes in land use responsible for the net *emissions* of carbon from the tropics are different from the changes in land use responsible for the net *sinks* for carbon in temperate zone and boreal forests. In the tropics, the dominant mechanism determining the net flux of carbon from land-use change is deforestation. Outside the tropics, the dominant mechanism is regrowth of forests from earlier changes in land use, management practices, and disturbances. This simplifying assumption is, of course, not strictly accurate; both clearing and regrowth operate in both regions. The simplification helps distinguish two different requirements in measuring/monitoring biomass.

Tropical forests

Although a number of forest inventories have been carried out in tropical forests, there remain large areas in the tropics where such inventories are out of date, incomplete, or entirely lacking. Many individual plots have been sampled, but extrapolating the results to an entire region is problematic. A comparison of seven approaches for mapping biomass in the Brazilian Amazon, for example, revealed not only a wide range in estimates of total biomass (greater than a factor of two between the lowest and highest estimates), but also no agreement as to where the largest and smallest forests existed (Houghton *et al*., 2001). Moreover, the estimates were largely for intact, or undisturbed forests, while both natural disturbances and human activities add variability to the distribution of biomass.

Despite variable forest inventories in the tropics, the FAO's three Forest Resource Assessments (FRAs) provide estimates of average country-level growing stocks ($\mathrm{m^3\,ha^{-1}}$) and/or biomass ($\mathrm{Mg\,ha^{-1}}$) in 1980, 1990, and 2000 (FAO/UNEP, 1981; FAO, 1993, 1995, 2001, respectively). The most interesting aspect of the estimates is that average forest biomass appears to have changed significantly in two of the three tropical regions (Table 1) (Fig. 2). Estimates of biomass declined each decade in Asian forests. The estimate in 2000 is nealy half of what it was in 1980. In contrast, estimates of forest biomass for Latin America increased each decade. In Africa, estimates of forest biomass varied over the three assessments but show no long-term trend.

These estimates of average regional biomass from the FAO assessments are based on area-weighted, country-level means. The country-level means, in turn, were determined from forest inventories. The problems, uncertainties, and errors result from these inventories. In many tropical countries, forest inventories are few in number (or nonexistent) and may not be representative of the country's forests.

The estimates of average biomass given in the FAO assessments are lower than the estimates used in calculating the flux of carbon from changes in land use (Achard *et al*., 2002, 2004; DeFries *et al*., 2002; Houghton, 2003). Achard *et al*. (2004) used estimates of aboveground biomass from Brown (1997) and increased them by 20% to account for belowground biomass. DeFries *et al*. (2002) and Houghton (2003) used biomass values from Houghton & Hackler (2001). Although the estimates of biomass used by the three studies vary, a direct comparison is difficult because the number and types of forests differ among the analyses. The simplest comparison is obtained by dividing the annual flux of carbon obtained in each study by the area deforested. The resulting quotient (in units of $\mathrm{Mg\,C\,ha^{-1}}$) is not a true measure of average biomass because, in addition to the carbon lost through deforestation, the flux (numerator) includes the uptake of carbon in regrowth as well as the emissions of carbon from soils and

Table 1 (A) Areas of natural and plantation forests (10^6 ha) and (B) average biomass of natural forests (Mg C ha^{-1}) in tropical regions (derived from the most recent FAO forest resource assessments)*

	1980		1990		2000	
Region	Natural forest	Plantation forest	Natural forest	Plantation forest	Natural forest	Plantation forest
(A) Forest area (10^6 ha)						
Asia	362	5	323	21	264	55
Africa†	732	2	692	3	636	6
Latin America†	1078	5	1004	8	952	8
Total tropics†	2172	12	2019	32	1852	69

Region	1980	1990	2000
(B) Average biomass of natural forests (MgC ha^{-1})‡			
Asia	127	104	70
Africa†	62	58	67
Latin America†	81	100	118
Area-weighted mean for all tropics†	82	86	94

*The areas are not those reported in each of the 1980, 1990, and 2000 FAO forest resources assessments (FRAs). Rather, we reconstructed the earlier areas on the basis of data in the more recent, revised assessments. The areas of forest in 1990 and 2000 were from the 2000 FRA, and the area in 1980 was calculated from the deforestation reported for the 1980s added to forest area in 1990. Given the substantial revisions in subsequent FRAs, we assumed that changes in forest area were better known than forest area, itself. Natural and plantation forest areas for 2000 were obtained from the 2000 FRA. Natural forest area for 1990 was calculated as the difference between total forest area in 1990 (from FRA, 2000) and plantation area in 1990 (from FRA, 1990) (Matthews, 2001 used the same approach). Plantation area in 1980 was obtained from the 1980 FRA. It is noteworthy that two different reports of the 1990 FRA (FAO, 1993, 1995) report different areas in plantations. The estimates in FAO (1995) are $\sim$ 70% of those in FAO (1993) because, on average, only 70% of established plantations survived (FAO, 1993). The areas in plantations shown here are from FAO (1995); they include the 70% reduction. Because we used these plantation areas to infer rates of change in natural forests, estimates of annual deforestation (of natural forests) are 1.1, 0.2, and 0.8×10^6 ha higher in Asia, Africa, and Latin America, respectively, than they would be without the 70% correction to 1990 plantation areas.

†In Africa, three nontropical countries, Lesotho, South Africa, and Swaziland, are included, while the six countries of northern Africa are not. In Latin America three nontropical countries, Argentina, Chile, and Uruguay, are included. The addition of these countries in Latin America increases the annual rate of deforestation (of natural forests) by 0.8×10^6 ha above the FAO (2001) rate of tropical deforestation. The different group of countries in Africa has no net effect.

‡Values were calculated from country means weighted by forest area. We converted aboveground biomass (from the FRAs) to units of total carbon by adding an additional 20% for roots and by multiplying by 0.5 for carbon content. For 1980, country-level estimates of average wood volume (m^3 ha^{-1}) were converted to estimates of average aboveground biomass with ratios (Mg m^{-3}) reported in the 2000 FRA.

(sometimes) degradation. Nevertheless, it provides an integrated measure of average carbon lost per hectare. The quotients (128, 138, and 145 for Achard *et al.*, 2004, DeFries *et al.*, 2002, and Houghton, 2003, respectively) are higher than the averages reported in FAO assessments (weighted means for all the tropics are 82, 86, and 94 for the 1980, 1990, and 2000 assessments, respectively) (Table 1).

A more precise comparison of estimates of biomass is shown in Fig. 2. The estimates from the FAO are consistently lower than the estimates Houghton (2003) used to calculate the flux of carbon from changes in land use. The trends in biomass are qualitatively similar, increasing in Latin America and falling in tropical Asia. While the declines in Asia are remarkably similar, the increase reported by FAO for Latin America is steeper than that attributable to changes in land use (Houghton, 2003). In tropical Africa, the trends between 1990 and 2000 are reversed: the modeled results (Houghton, 2003) show a continuing decline in average biomass, while FAO reports an increase.

Houghton's estimates of average regional biomass (Fig. 2) are determined by two processes. First, the initial ($\sim$ 1850) biomass for a region is estimated for broad categories of forest on the basis of reviews in the ecological literature (e.g., Olson *et al.*, 1983; Brown *et al.*,

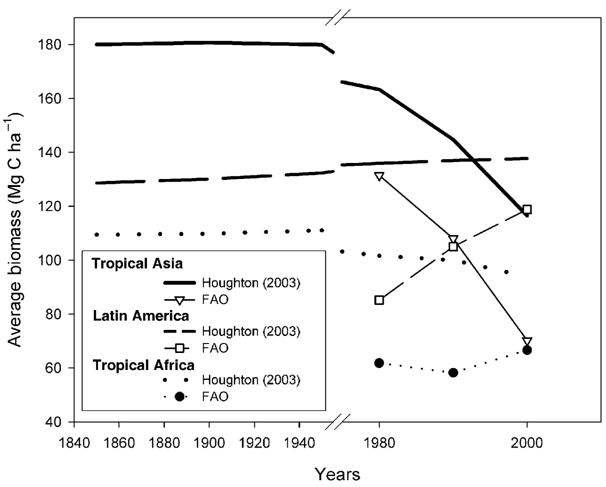

Fig. 2 Estimates of the average biomass of tropical forests, as reported by the FAO (1980, 1990, and 2000 assessments) (light lines) and as modeled from changes in land use (1850–2000) (Houghton, 2003) (heavy lines). Note the change in temporal scale between 1940 and 1980.

1989). Second, in the course of a model simulation the average biomass changes as primary forests are converted to secondary forests, and as deforestation removes forests of different mean biomass.

The apparent changes in biomass reported by the FAO assessments may, similarly, reflect the effects of human activity. On the other hand, they may reflect improved information, as more forests were inventoried after 1980 and the information became available. Either interpretation has consequences for carbon emissions. The interpretation that the changes reflect improved information is consistent with the most recent assessment (FAO 2001), which states (p. 20) that changes in woody biomass within the forests of developing (i.e., tropical) countries are not known. Thus, differences among assessments must reflect improved estimates, and the most recent assessment must contain the best estimate. If the latest FAO estimate is correct, current estimates of carbon emissions from land-use change in the tropics (Achard *et al.*, 2002; DeFries *et al.*, 2002; Houghton, 2003) are overestimates, because those analyses overestimated mean forest biomass.

The second interpretation, that the changing estimates from the FAO reflect real on-the-ground changes, could be explained by two types of change. First, average forest biomass would change if deforestation occurred in forests that were systematically higher (or lower) in biomass than the average. Second, average biomass would also change, downward if forests were being degraded (through shifting cultivation, fires, logging, grazing, or fragmentation), or upward if forests were growing (that is, if growth exceeded degradation).

If the decrease in biomass reported for tropical Asian countries is assumed to have resulted only from the loss of high-biomass forests, the biomass of the forests deforested would have to have averaged 530 Mg ha^{-1}. While forests with such a high biomass exist, it seems unlikely that deforestation would have been limited to those forests. It is more likely that most of the decline in average forest biomass in Asia (an 18% decline in the 1980s and a 35% decline in the 1990s) was the result of degradation (primarily logging). Logging converts primary forests of high biomass to secondary forests of low biomass. Despite its claim that changes in the biomass of forests are not known, the FAO (2001) reports that forests are being degraded (as well as deforested) throughout the tropics. Hence, a trend of decreasing biomass would be expected in Asia, where logging removes and damages more biomass than in other regions (FAO, 1993), and where the total forest area is smaller (Table 1).

In Africa, the 6% decline in average forest biomass during the 1980s could be explained either by deforestation of forests averaging 208 Mg ha^{-1} (the overall average was 103 Mg ha^{-1}), by degradation, or by some combination of the two. Again, degradation seems more likely. The apparent increase in average forest biomass during the 1990s, on the other hand, could have occurred if deforestation was of low-biomass forests (averaging 62 Mg ha^{-1}, in contrast to an average of 103 Mg ha^{-1}), or if growth exceeded degradation. The net increment in aboveground biomass needed to explain the increase, would have to have been 0.54 Mg ha^{-1} yr^{-1}. Again, while the rate is entirely possible, the reported changes for African biomass, down during the first decade, and up in the second, suggest uncertain estimates rather than real changes on the ground.

The increase in average biomass reported for Latin America cannot be explained through the loss of low-biomass forests alone. Without much higher rates of deforestation than reported, the average biomass of the forests deforested would have to have been negative to yield the reported increase in average biomass.

If the apparent increase in Latin American average biomass were to be explained through growth, average rates of net growth would have to have been 2.2 and 1.5 Mg biomass ha^{-1} yr^{-1} in the 1980s and 1990s, respectively. Accounting for logging and other forms of degradation would require even larger rates of growth. While such rates of growth are possible, a more likely explanation for the apparent increase in biomass is an expanding set of measurements rather than real on-the-ground changes. It is worth pointing out, however, that two independent analyses have found increased rates of growth in Amazonian forests that were not found in other tropical regions. A global analysis of changes in environmental variables over the period 1982–1999 predicted a global increase in net primary production that was largely in Amazonia (Nemani *et al*., 2003), and repeated measurements in undisturbed forests throughout the tropics found an increase in the biomass of Amazonian forests but not in tropical Africa or Asia (Phillips *et al*., 1998). The findings remain controversial (Clark, 2002; Phillips *et al*., 2002; Baker *et al*., 2004; Clark, 2004).

A modeling experiment

To determine how uncertainties in rates of deforestation and in average forest biomass affect estimates of carbon emissions, we conducted a series of sensitivity tests with a carbon model. The model (the same as used by Houghton, 2003) calculates the net flux of carbon from changes in land use (deforestation, establishment of plantations, and logging). For each of the three tropical regions, we conducted five experiments: a reference analysis (Houghton, 2003), two alternative rates of deforestation, and two alternative estimates of biomass. The rates of deforestation were those reported by FAO (2001) (used by Houghton, 2003), Achard *et al*. (2002), and DeFries *et al*. (2002). The three tests of biomass included the initial estimates compiled by Houghton (2003) (and used subsequently by DeFries *et al*., 2002), and two tests with estimates from the FAO assessments (Table 1). In one test, initial forest biomass (1850) was adjusted to yield an average forest biomass in 2000 similar to the FAO estimate for 2000 (FAO, 2001). In the last test, the initial biomass was adjusted to yield the average biomass reported by FAO in 1980 (FAO/UNEP, 1981). In this last experiment, the proportions of low- and high-biomass forests deforested after 1980 were modified (from Houghton, 2003) to try to match the changes in biomass as reported in the three FAO assessments.

The simulations of land-use change varied among regions but not across experiments. In tropical Asia, for example, all simulations included deforestation, establishment of plantations, and logging; in Africa, neither plantations nor logging were simulated (only deforestation); and in Latin America deforestation and logging were included, but not plantations. These regional differences reflect our past efforts in the analyses; current efforts are focused on Africa.

In each experiment, annual rates of land-use change were used to start hectares of forests along trajectories of change in carbon stocks (as in Fig. 1). Rates of logging and rates of plantation establishment were the same in all experiments. For the reference experiment, rates of deforestation (and the establishment of plantations) were determined from the changes in area reported in the most recent FAO assessments (Table 1). The initial carbon stocks varied in experiments 4 and 5, and rates of deforestation varied in experiments 2 and 3. In experiment 2 (the 'Achard' experiment), rates of deforestation in the 1990s were those reported by Achard *et al*. (2004). The rates before 1990 were reduced from the rates reconstructed by Houghton (2003) by the ratio of Achard's rates of deforestation in the 1990s to Houghton's rates in the 1990s. Likewise, in experiment 3 (the DeFries experiment), the rates between 1980 and 2000 were the average annual rates reported by DeFries *et al*. (2002). Before 1980, the annual rates of deforestation were proportional to the rates of Houghton's reconstruction, where the proportion was based on the ratio of DeFries' 1980s and 1990s rates of deforestation to Houghton's 1980s and 1990s rates.

As expected, the results of the experiments show that the flux of carbon is sensitive to both rates of deforestation and forest biomass (Fig. 3). The three estimates of biomass used in the tests generated a range of flux estimates nearly as broad as the range generated by different estimates of tropical deforestation (Table 2). The flux of carbon calculated from changes in land use (three rates of deforestation) varied between 2.15 and 0.84 Pg C yr^{-1} for the 1990s (a range of 1.31 Pg C yr^{-1}). The flux of carbon calculated using three estimates of biomass varied between 2.15 and 1.20 Pg C yr^{-1} (a range of 0.95 Pg C yr^{-1}). The range attributed to uncertain estimates of biomass is probably an underestimate because the tests used average values of biomass. On the contrary, accurate estimates of carbon flux require, not average values over large regions, but the biomass

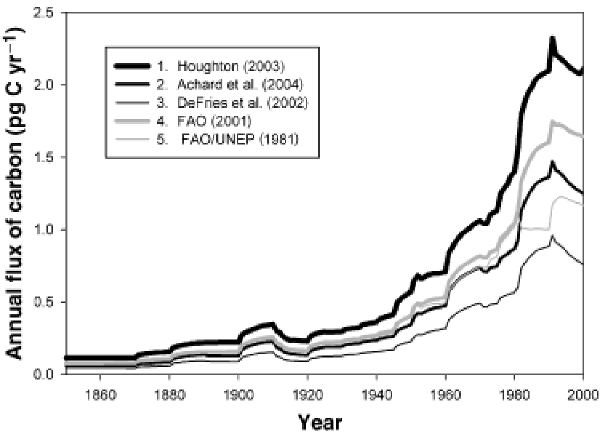

Fig. 3 Annual emissions of carbon from land-use change in the tropics according to alternative rates of tropical deforestation and alternative estimates of average forest biomass.

Table 2 Rates of tropical deforestation, average biomass of tropical forests, and average annual flux of carbon from tropical deforestation in the 1990s

Test	Rate of deforestation (10^6 ha yr^{-1})	Average biomass* (Mg C ha^{-1})	Net flux (Pg C yr^{-1})
1. Houghton (2003)	14.8	129	2.15
2. Deforestation from Achard *et al.* (2004)	8.6	129	1.34 (1.1)
3. Deforestation from DeFries *et al.* (2002)	6.5	128	0.84 (0.9)
4. Biomass similar to FAO (2001) estimate	14.8	100	1.69
5. Biomass similar to FAO/UNEP (1981) estimate	14.8	84	1.20

The values in parentheses are the results reported by Achard *et al.* (2004) and DeFries *et al.* (2002).
*Average biomass refers to all forests extant in 2000.

Table 3 Areas, total carbon stocks, and average carbon stocks in the biomass of forests and woodlands in the northern temperate and boreal zones in 1990 (from Goodale *et al.*, 2002)

Region	Forest area (10^6 ha)	Other woodland area (10^6 ha)	Forest living biomass (Pg C)	Woodland living biomass (Pg C)	Average forest biomass (Mg C ha^{-1})	Average woodland biomass (Mg C ha^{-1})
Canada	316	88	12.9	1.6	40.8	18.2
United States	212	86	13.3	3.3	62.7	38.4
Europe	149	46	7.7	0.2	51.7	4.3
Russia	821	66	33.7	0.6	41.0	9.1
China	119	39	4.6	0.6	38.6	5.0
Other*	92	16	4.7	na	51.1	na
Total	1711	339	77	...	45.0	...

*Countries included: Japan, North Korea, South Korea, Mongolia, Latvia, Lithuania, Estonia, and the Commonwealth of Independent States other than Russia.

of the forests actually deforested and logged. Thus, uncertainty in biomass probably contributes as much error to estimates of tropical carbon flux as uncertainty in rates of deforestation. These uncertainties could be reduced if forest biomass was determined at a spatial resolution consistent with the resolution of land-use change; that is, at the level of ~ 1 ha (100 m resolution).

Experiment 5 was unable to reproduce the trends in forest biomass reported by the FAO for Latin America and Africa. The total areas of forest were large relative to rates of clearing, and thus, the average biomass of all forests was not sensitive to the biomass of the forests deforested. The calculated net flux of carbon, however, was reduced significantly by deforesting forests with low biomass. The results of the experiments confirm, first, that carbon emissions are sensitive to the biomass of the forests deforested and, second, that FAO's reported changes in average biomass for tropical America and Africa must largely reflect revised estimates rather than real on-the-ground changes.

It is important to recognize that the interannual variability in Fig. 3 is not the result of interannual variability in deforestation rates or climatic variables. Rates of deforestation were constant within each decade, and the bookkeeping model does not include the effects of environmental variables, such as CO_2, N deposition, or climate (e.g., El Niño events). Instead, interannual variability in carbon emissions (for example, the spike in the early 1990s) results from abrupt transitions in deforestation rates from one decade to the next. The interannual variability in Fig. 3 is largely an artifact of the bookkeeping approach.

In sum, the emissions of carbon from tropical deforestation depend to a large extent on the biomass of the lands deforested. The errors in calculated emissions of carbon result as much from uncertain estimates of biomass as they do from uncertain rates of deforestation. We do not know whether tropical deforestation occurs in forests of high-, low-, or average biomass.

Temperate zone and boreal forests

The biomass of temperate zone and boreal forests is better known than the biomass of tropical forests because most temperate zone and boreal forests have been inventoried. A recent study by Goodale *et al.* (2002) summarized forest area and biomass for these forests (Table 3). The summary updates an earlier analysis by Dixon *et al.* (1994), especially in China and

Russia, where more recent estimates of biomass are considerably lower.

The accuracies of these forest inventories probably vary among countries. For permanent sample plots in the south-eastern US, the error calculated for the total volume of growing stock (trees) was within 1.1%, while *changes* in the stock were within ±40% (Phillips *et al.*, 2000). For the private timberlands of the US (~ 70% of US forest area), including understory vegetation, litter, and soil as well as in trees yielded an estimated uncertainty of 9% for carbon stocks and about 50% for carbon flux (at 95% confidence) (Heath & Smith, 2000). The absolute uncertainties were 2 Pg C (out of 22.4 Pg) and 0.029 $\mathrm{Pg\,C\,yr^{-1}}$ (out of 0.058 $\mathrm{Pg\,C\,yr^{-1}}$), respectively.

It is unlikely that satellite data will yield estimates of biomass that are more accurate than ground measurements, and, if not, one might question whether it is worth using satellite data outside the tropics. It is important to recognize, however, that forest inventories have been designed to give total volumes of growing stock (and changes) at the level of countries, states, or other administrative units. They are based on sample plots. As stated previously, they do not provide the spatial distribution of biomass at a resolution compatible with changes in land use and management. Thus, even if satellite data are not as accurate for estimating total biomass *at the plot level* as existing ground-based inventories, the wall-to-wall coverage from satellite data would be a valuable addition for calculating the emissions of carbon from disturbance, as well as for recording the times and locations of disturbance.

Another major difference between tropical and nontropical forests (besides the extent of inventories) is that forests in the northern mid-latitudes are not changing in area, for the most part, but in carbon stocks per unit area. The forests are generally recovering from earlier changes in land use and management, for example, logging, fire suppression, and the abandonment of agriculture (Houghton *et al.*, 1999). The carbon sinks resulting from this recovery have been difficult to quantify with optical satellite data because 'hidden' increments in biomass continue beneath a closed canopy, and because the changes in land use that initiated recovery often preceded the satellite record. Deforestation is readily apparent with optical data; reforestation is less so, particularly after canopy closure. *Thus, the reason for knowing the spatial distribution of biomass in northern forests is different from the reason in the tropics*. In the tropics, the need is to link biomass to deforestation. In temperate zone and boreal forests, the need is to estimate changes in aboveground biomass.

With a single 'look' from satellite, forest growth or biomass increment might be calculated from a relationship between age (or height or biomass) and increment. However, not all of the spatial variation in biomass within a forest landscape is related to age. Yield tables relate growth to age, but only when site or productivity class is known. What are the relative effects of age and microenvironmental factors in explaining spatial variations in biomass and growth? How does spatial variability vary with spatial scale? What pixel size is appropriate for these scales of variability (see 'What are the spatial scales of biomass variability?')? These questions will need to be addressed in the design of a satellite to measure biomass.

With two or more 'looks' from space, changes in biomass might be determined 'directly'. And, if aboveground biomass could be determined directly from space, an alternative, more direct, method could be used to calculate sources and sinks of carbon. The approach used to date, based on documenting changes in land use, would no longer be necessary. If changes in biomass could be determined directly, one would see any and all changes in aboveground biomass, whether caused by human activity or not. The measured change would be an estimate of net change in aboveground carbon stocks, and, to a first approximation, net flux of carbon between land and atmosphere. However, at least two qualifications need to be added. First, direct measurement of change in aboveground biomass would miss changes in fallen wood, belowground carbon, and in harvested products (Fig. 1) (see also the section 'Importance of biomass' described later), although these could be modeled as they are at present. Second, measurement of change in aboveground biomass would also lack the ability to attribute a mechanism to the observed changes; that is, it would not distinguish between the direct and indirect effects of human activities (e.g., recovery from logging, and $\mathrm{CO_2}$ fertilization, respectively). For that distinction, one would still want to document the location, date, and, especially, the cause of disturbance (natural or human induced).

In sum, carbon sinks from regrowth in temperate zone and boreal forests will be underestimated if past disturbances were not documented (e.g., if they were initiated before the satellite record). On the other hand, this bias vanishes if height and/or biomass can be determined 'directly' from space. With repeated looks, one should, in theory, observe both growth and degradation of aboveground biomass, although distinguishing the causes of growth (regrowth vs. enhanced growth) will still require information about management.

These conclusions for temperate zone and boreal forests are different from the conclusions for tropical forests, above. The difference is largely artificial, however. Despite the different processes *dominant* in the two regions, both processes occur in both regions. That is, there are regrowing forests in the tropics, and there is deforestation (or logging, anyway) outside the tropics. Measurement of biomass and of changes in biomass is required in both regions for evaluating the role of forests in the global carbon balance.

How well do we have to know the biomass of the world's forests?

The answer depends, of course, on why we want to know biomass. Four subquestions are addressed below.

What are the magnitudes of terrestrial sources and sinks of carbon?

The global net terrestrial carbon *sink* averaged 0.8 (± 0.8) Pg C yr^{-1} during the 1990s (Table 4). Estimates of net *emissions* from land-use change vary between about 1 and 2 Pg C yr^{-1}. If these estimates are correct, the residual terrestrial sink is 2–3 Pg C yr^{-1}. If this sink has accumulated in aboveground forest biomass, the average sink would be 0.5–0.8 Mg C ha^{-1} yr^{-1} (for 3.869×10^9 ha of forests; FAO, 2001), or about 1% of the carbon in aboveground biomass (global average forest biomass is 109 Mg ha^{-1}, half of it carbon) (FAO, 2001). If some of the carbon has accumulated outside of forests or in belowground pools, the accumulation in aboveground biomass would be correspondingly less. If, on the other hand, soils have lost carbon as a result of warming, the sink in aboveground biomass might be larger. A 1% yr^{-1} change in forest biomass would certainly not be seen in successive 'looks' a year apart if the change were widely distributed, but it might be seen in 10–20 years or might be seen if it were concentrated in small regions.

The annual increase in aboveground biomass needed to accommodate the global carbon sink is larger if the sink is concentrated in northern mid-latitude forests. The total sink in that region is ~ 2 (± 0.8) Pg C yr^{-1} (Table 4), and if all of it accumulated in forest biomass (77 Pg C) (FAO, 2001), the average annual sink would be 2.7% of the stocks (or 1.2 Mg C ha^{-1} yr^{-1}). Such a relative increase in aboveground biomass might be observed directly from space over a 10-year period.

Much of the northern mid-latitude sink may not be in forests, however. According to budgets based on data from forest inventories, the annual sink in northern mid-latitude forests is estimated to have been 0.65 Pg C in 1990 (Goodale *et al.*, 2002). The estimate, based on forest inventories, is only a fraction of the sink inferred from atmospheric data and models (2.1 (± 0.8) Pg C yr^{-1}) (Table 4), suggesting that more than half of the northern terrestrial carbon sink is in nonforest ecosystems. Furthermore, the estimated sink of 0.65 Pg C yr^{-1} includes changes in above- and belowground biomass, coarse woody debris, soils, and wood products. The sink in living biomass (~ 80% of which is aboveground), was only 0.2 Pg C yr^{-1}, and it was not evenly distributed. Canadian and Russian forests lost 0.08 Pg C from biomass in 1990, while forests in the US, Europe, China, and other northern regions gained a total of 0.28 Pg C (Goodale *et al.*, 2002). Needless to say, there are both sources and sinks of carbon in the forests of each country. In fact, there are undoubtedly areas where site-specific sources and sinks of carbon are large enough to be observed from space over a 2–3-year interval. Thus, despite the fact that measuring biomass from space will

Table 4 Estimates of the annual terrestrial flux of carbon (Pg C yr^{-1}) in the 1990s according to different methods

	O_2 and CO_2	Inverse calculations CO_2, $^{13}CO_2$, O_2	Forest inventories	Land-use change
Globe	−0.7 (± 0.8)*	−0.8 (± 0.8)†	–	1–2‡
Northern mid-latitudes	–	−2.1 (± 0.8)§	−0.65¶	−0.03 (± 0.5)‡
Tropics	–	1.5 (± 1.2)‖	−0.6 (± 0.3)**	0.5 to 3.0††

Negative values indicate a terrestrial sink.
*Plattner *et al.* (2002).
†−1.4 (± 0.8) from Gurney *et al.* (2002) reduced by 0.6 to account for river transport (Aumont *et al.*, 2001).
‡Achard *et al.* (2002), DeFries *et al.* (2002), Houghton (2003).
§−2.4 from Gurney *et al.* (2002) reduced by 0.3 to account for river transport (Aumont *et al.*, 2001).
¶Goodale *et al.* (2002).
‖1.2 from Gurney *et al.* (2002) increased by 0.3 to account for river transport (Aumont *et al.*, 2001).
**Undisturbed forests only: Phillips *et al.* (1998) (challenged by Clark, 2002).
††0.9 (range 0.5–1.4) from DeFries *et al.* (2002), 1.1 from Achard *et al.* (2004), 2.2 (± 0.8) from Houghton (2003), 2.4 from Fearnside (2000).

not be as precise as measurements on the ground, satellite data might prove as useful as forest inventory data if the sources and sinks of carbon are not evenly distributed (see 'How are sources and sinks of carbon distributed over the earth's surface?').

There are areas where measurement by satellite will be more informative than ground-based inventory data. These areas include the remote forests of Canada and Russia, where inventories are not conducted, and nonwooded lands that are being invaded by woody vegetation (woody encroachment) (Houghton *et al*., 1999; Pacala *et al*., 2001; Asner *et al*., 2003). Ecosystems experiencing woody encroachment are not included in the US Forest Service's forest inventories because they are not (yet) forests. If a satellite were designed to detect woody encroachment, the data would provide a source of information that has hitherto been restricted to geographically limited ground studies (Asner *et al*., 2003).

Whether or not a carbon sink exists in the tropics is uncertain. The net flux of carbon inferred from atmospheric measurements and models is a source of 1.5 ($\pm$ 1.2) Pg C yr^{-1} when river transport is taken into account (Table 4). Estimates of emissions from deforestation are of a similar magnitude, suggesting no significant carbon sink. The uncertainties are large, however. If the emissions from land-use change are at the high end of the range, an additional carbon sink would be required (Houghton, 2003). Repeated measurements on permanent plots of old-growth forests in Amazonia sometimes show an increase in biomass over the last two decades (Baker *et al*., 2004), and sometimes, do not (Clark, 2004). Interestingly, if the net flux of carbon is at the high end of the range, and the land-use flux is at the low end, the carbon community will be looking for a missing carbon source.

How are sources and sinks of carbon distributed over the earth's surface?

How well we have to know the biomass of the world's forests depends on how the sources and sinks of carbon are distributed over the land surface. Changes in carbon stocks will be difficult to measure from space if they are evenly distributed over large regions (including nonforests), or if they are in belowground components (coarse woody debris, roots, soils). As discussed above, only about half of the northern mid-latitude terrestrial carbon sink seems to be in forests. If some of the nonforest sink is in woody encroachment, it may be measurable from space. If it is agricultural soils, it will probably not be.

However, the northern terrestrial sink is not evenly distributed. As described above, forest inventories indicated a net sink in the biomass of the US, Europe, and China, and a net source from the biomass of Canada and Russia. The variability raises the possibility that the major terrestrial sources and sinks of carbon may be measurable from space. Figure 1b shows the annual sources and sinks of carbon on a hectare of land as a result of harvest and regrowth of a forest. The same figure can be viewed as the distribution of different aged forests on a landscape (Fig. 4). In this case, 1–5-year-old forests are a strong source of carbon, 10- to ~ 40-year-old forests are a strong sink for carbon, and forests older than ~ 50 years are weak sinks. What if 90% of the net terrestrial flux of carbon occurs on lands where the annual changes are large enough to be inventoried from space? Such a high percentage would make a monitoring program more feasible (and appealing) than a low percentage. At present, we do not know what fraction of the world's forests is growing and what fraction is 'grown'. Below some threshold of change, forests will appear as though their carbon stocks are not changing. The threshold depends not only on the sensitivity of a sensor, but on the frequency and intensity of disturbances on the landscape, something about which we know very little in most regions of the world. Is the terrestrial carbon sink small per unit area but distributed over very large areas, or is most of it in areas characterized (and identifiable) by rapid growth rates? A satellite might be able to answer these questions.

Even if increments in biomass are generally too small to be measurable annually from space, repeated looks over 3–5-year intervals would presumably identify areas with growth. And such intervals are probably appropriate for changes in biomass, which are not particularly important in accounting for interannual variability in atmospheric growth rates of CO_2. Interannual variability in CO_2 flux is large relative to the average growth rates of trees (Barford *et al*., 2001). Most of the short-term variations in flux result from carbon pools of high turnover; for example, foliage, litter, and microbial processes. Thus, except for young, vigorously growing forests or recently disturbed forests, aboveground biomass is appropriately measured at 5–10-year intervals. The interval should not be so long as to miss both the disturbance and recovery of a system, however.

What are the spatial scales of biomass variability?

Biomass varies across broad environmental gradients of moisture and temperature, and it varies at fine scales as a result of disturbances. Brown (1997) and colleagues have pioneered approaches for distributing biomass at broad scales, from large regions, such as tropical Africa

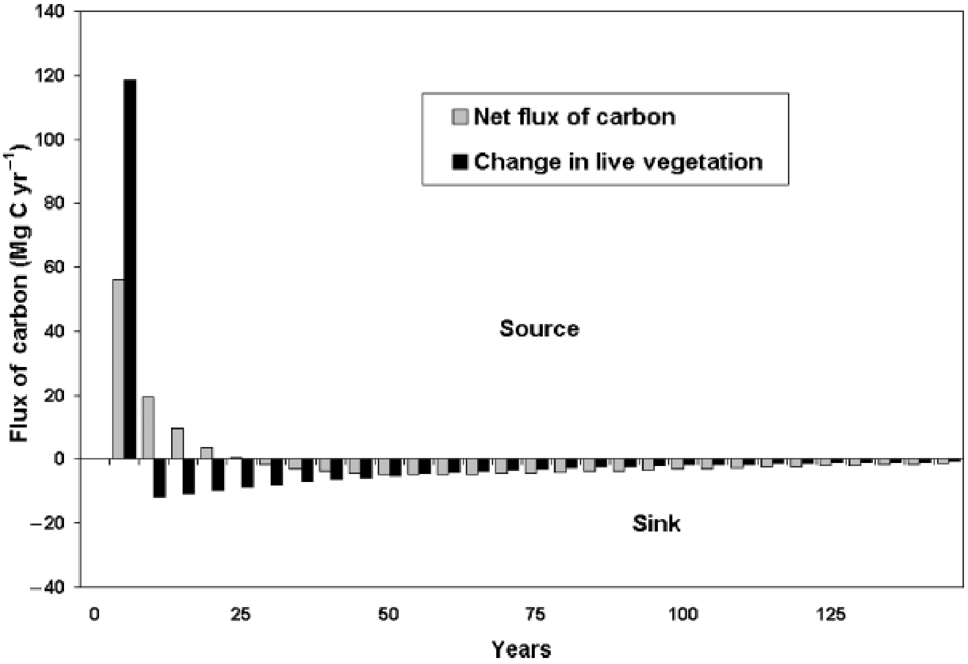

Fig. 4 Annual changes in the carbon pools of forest patches of different age in a hypothetical landscape. Open bars show the net flux from all components of the ecosystem; closed bars show the net changes in living biomass (drawn negatively for comparison with estimates of flux).

(Gaston *et al*., 1998) and tropical Asia (Brown *et al*., 1993, Iverson *et al*., 1994) to smaller regions, such as Peninsular Malaysia (Brown *et al*., 1994). Such coarse-scale mapping clearly provides estimates of mean biomass that are more constrained than averages for entire biomes. But are they constrained enough? Human-induced, as well as natural, disturbances create patches such that spatial variability may be as great between adjacent hectares as it is over thousands of kilometers. From the perspective of the discussions above, variability at fine spatial scales is important.

There are at least two considerations for selecting the appropriate pixel size for measuring biomass from space. For determining the biomass of the forest actually deforested, logged, or otherwise disturbed, the pixel size should be close to the size of the disturbance (25–100 m). In areas without disturbance, the pixel size may be larger, large enough to capture an 'average' or representative biomass. For example, tropical forests often have a few large trees with a disproportionate share of aboveground biomass. Small plots either include a large tree (and overestimate biomass) or do not (and underestimate biomass). The appropriate plot (pixel) size should capture large trees in proportion to their abundance (100–200 m resolution). Because both types of variability are important, the required pixel size should probably not exceed 100 m. In the best of worlds, the pixel size for measuring biomass would be of the same spatial (and temporal) resolution as the pixel size for measuring disturbance. Indeed, as noted above, both biomass and disturbance can be obtained with the same satellite.

How important is biomass relative to coarse woody debris, soils, and wood products in accounting for the entire flux of carbon between land and atmosphere?

The importance of biomass, relative to other carbon pools, will depend on the dominant types of land use, the region and the time interval. In the short term the bias in estimating net carbon flux from biomass alone can be seen in Fig. 4. In comparison with the net flux based on full carbon accounting, the change in living biomass, alone, is exaggerated, both the loss in the year of harvest and the growth in the first 10 years of recovery. Lag times in the decomposition and recovery of coarse woody debris and soil carbon tend to dampen the response from biomass alone.

In the longer-term, the nonbiomass components of ecosystems have been less important than the biomass components. For the period 1850–1990, the net loss of carbon from biomass accounted for 89% of the calculated net flux of carbon from land-use change (Houghton, 1999). In comparison, soil carbon accounted for 28% of the net loss. The two pools sum to more than 100% of the net loss because wood products and slash (coarse woody debris) accumulated carbon and offset the long-term net release by 14% and 3%, respectively. Biomass is relatively more important in the tropics and less important outside because the per hectare averages are generally higher in the tropics (Tables 1 and 3).

Other, more direct measurements, also suggest that changes in soil carbon, slash, and wood products are of secondary importance. For most changes in land use, the per hectare losses and gains of carbon in soil are small relative to the changes in biomass (Houghton & Goodale, 2004). Thus, although soils hold two to three times more carbon globally than biomass, they contribute relatively little to sources and sinks of carbon from land-use change. Their importance as a sink has also been small in the few places where fluxes have been measured (Barford *et al*., 2001; Schlesinger & Lichter, 2001).

Summary

In the tropics, biomass is of primary importance: knowing it allows calculation of the amount of carbon lost with deforestation. In northern temperate zone and boreal forests, biomass is secondary. Knowing the *rate of change* in biomass, however, and the reasons for its change are of primary importance. Such information would enable current and near-future changes in carbon stocks (sources and sinks) to be inferred.

How well is biomass known presently? In temperate zone and boreal forests, the average aboveground biomass is well known for most administrative units as a result of systematic sampling for inventories. The biomass of individual stands or plots (that is, the spatial distribution of biomass) is generally not known, however. For most tropical forests, neither the averages nor the spatial distribution of biomass are known.

How well are changes in biomass known? The answer is similar. For temperate zone and boreal forests, decadal changes are reasonably well characterized, although not with the same relative precision as the stocks themselves. And in the tropics, changes in biomass are not known except in a few permanent plots (Phillips *et al*., 1998, 2002; Clark, 2002; Baker *et al*., 2004). The current uncertainty in tropical forest biomass is as important as the rate of deforestation in reducing the error of estimated net fluxes of carbon.

How well do we have to measure biomass and changes in it to improve our understanding of the global carbon balance? A quantitative answer is difficult. In the tropics, an uncertainty of ~ 50% in *average* biomass translates into an uncertainty of about 80% in estimates of flux (Table 2), and the uncertainty of biomass for the forests actually deforested is probably much greater. The latter is a more troublesome error because it has the potential to introduce bias. If aboveground biomass could be estimated to within 10–25%, the error of flux estimates might be reduced to a similar range (10–25%), well below the current uncertainty of over 100%. It should be clear that a satellite capable of measuring biomass would simultaneously measure and map deforestation and degradation, thus reducing uncertainties in both deforestation rates and biomass.

Satellite-based measurement of biomass in temperate zone and boreal lands will not necessarily result in improved estimates of *average* biomass, but will provide, first, the spatial distribution of biomass and, second, estimates of change in ecosystems not included in forest inventories (Table 5). Examples include ‘other wooded lands’ and woody encroachment, as well as forests outside inventoried lands. In Canada and Russia, for example, there are large areas of inaccessible

Table 5 Strengths and weaknesses in measurement of aboveground biomass from space

Potential weaknesses in the use of satellites to measure biomass:

1. Measurement of biomass from space is unlikely to be as precise as existing inventory programs in temperate zone and boreal forests
2. Measurement of biomass from space is unlikely to be precise enough to see any but the largest changes over the short term (one to several years)
3. Measurement of biomass from space will miss the other terrestrial pools of carbon (fallen dead, belowground biomass, soil carbon, wood products)

Potential strengths in the use of satellites to measure biomass:

1. Satellite data will *map* biomass (not just provide averages as forest inventories do)
2. Satellite data will measure changes in woody biomass on lands not included in inventories (remote forests, other wooded lands, lands with wood encroachment)
3. Measurement of biomass from space has the potential to replace existing approaches for calculating carbon sources and sinks with an approach that includes more than land-use change
4. Measurement of biomass from space will show what fraction of the world’s forests is growing, and how that fraction varies regionally; that is, it will provide quantitative data on rates of disturbance

forests. As in the tropics, measuring changes 'directly' over a decade or so, would capture those ecosystems with the largest net fluxes of carbon. At present, we do not know what fraction of the net terrestrial flux is contributed by such ecosystems. To some extent, the answer will depend on the sensitivity of the satellite sensor; but it will also depend on the frequency of disturbance in forests. The latter is poorly known for many regions.

And, finally, what fraction of the total change in carbon stocks is not in aboveground biomass, but in coarse woody debris, soils, and wood products? Estimates based on land-use change suggest 10–35%. Full accounting for carbon will require a combination of direct measurement and modeling, but the largest changes in terrestrial carbon involve living biomass.

Acknowledgements

The author gratefully acknowledges the contributions of J. L. Hackler in carrying out the model simulations, and the comprehensive reviews and constructive comments from D. A. Clark, B. E. Law, and an anonymous reviewer. Research was supported by grants from NASA's programs in Terrestrial Ecology (NAG5-13351) and Land Cover/Land-Use Change (grant number NAG5-11286).

References

Achard F, Eva HD, Mayaux P *et al*. (2004) Improved estimates of net carbon emissions from land cover change in the tropics for the 1990s. *Global Biogeochemical Cycles*, **18**, GB2008, doi: 10.1029/2003GB02142.

Achard F, Eva HD, Stibig H-J *et al*. (2002) Determination of deforestation rates of the world's humid tropical forests. *Science*, **297**, 999–1002.

Asner GP, Archer S, Hughes RF *et al*. (2003) Net changes in regional woody vegetation cover and carbon storage in Texas drylands, 1937–1999. *Global Change Biology*, **9**, 316–335.

Aumont O, Orr JC, Monfray P *et al*. (2001) Riverine-driven interhemispheric transport of carbon. *Global Biogeochemical Cycles*, **15**, 393–405.

Baker TR, Phillips OL, Malhi Y *et al*. (2004) Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London*, **B359**, 353–365.

Barford CC, Wofsy SC, Goulden ML *et al*. (2001) Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. *Science*, **294**, 1688–1691.

Barlow J, Peres CA, Lagan BO *et al*. (2003) Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecology Letters*, **6**, 6–8.

Brown S (1997) *Estimating Biomass and Biomass Change of Tropical Forests: A Primer. FAO Forestry Paper 134*. FAO, Rome.

Brown S, Gillespie AJR, Lugo AE (1989) Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science*, **35**, 881–902.

Brown S, Iverson LR, Lugo AE (1994) Land use and biomass changes of forests in Peninsular Malaysia during 1972–82: use of GIS analysis. In: *Effects of Land Use Change on Atmospheric CO_2 Concentrations: South and Southeast Asia as a Case Study* (ed. Dale V.H.), pp. 117–143. Springer-Verlag, New York.

Brown S, Iverson LR, Prasad A *et al*. (1993) Geographic distribution of carbon in biomass and soils of tropical Asian forests. *Geocarto International*, **8**, 45–59.

Clark D (2002) Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecological Applications*, **12**, 3–7.

Clark DA (2004) Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. *Philosophical Transactions of the Royal Society of London*, **B359**, 477–491.

DeFries RS, Houghton RA, Hansen MC *et al*. (2002) Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 90s. *Proceedings of the National Academy of Sciences*, **99**, 14256–14261.

Dixon RK, Brown S, Houghton RA *et al*. (1994) Carbon pools and flux of global forest ecosystems. *Science*, **263**, 185–190.

Drake JB, Knox RG, Dubayah RO *et al*. (2003) Above-ground biomass estimation in closed-canopy Neotropical forests using lidar remote sensing: factors affecting the generality of relationships. *Global Ecology and Biogeography*, **12**, 147–159.

Eva HD, Achard F, Stibig H-J *et al*. (2003) Response to comment on 'determination of deforestation rates of the world's humid tropical forests'. *Science*, **299**, 1015b.

FAO (1993) *Forest Resources Assessment 1990. Tropical Countries. FAO Forestry Paper No. 112*. FAO, Rome.

FAO (1995) *Forest Resources Assessment 1990. Global Synthesis. FAO Forestry Paper No. 124*. FAO, Rome.

FAO (2001) *Global Forest Resources Assessment 2000, Main Report. FAO Forestry Paper 140*. FAO, Rome.

FAO/UNEP (1981) *Tropical Forest Resources Assessment Project*. FAO, Rome.

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.

Fearnside PM, Laurance WF (2003) Comment on 'determination of deforestation rates of the world's humid tropical forests'. *Science*, **299**, 1015a.

Flint EP, Richards JF (1994) Trends in carbon content of vegetation in south and southeast Asia associated with changes in land use. In: *Effects of Land Use Change on Atmospheric CO_2 Concentrations: South and Southeast Asia as a Case Study* (ed. Dale V.H.), pp. 201–299. Springer-Verlag, New York.

Gaston GS, Brown S, Lorenzini M *et al*. (1998) State and change in carbon pools in the forests of tropical Africa. *Global Change Biology*, **4**, 97–114.

Goodale CL, Apps MJ, Birdsey RA *et al*. (2002) Forest carbon sinks in the northern hemisphere. *Ecological Applications*, **12**, 891–899.

Gurney KR, Law RM, Denning AS *et al*. (2002) Towards robust regional estimates of CO_2 sources and sinks using atmospheric transport models. *Nature*, **415**, 626–630.

Heath LS, Smith HE (2000) An assessment of uncertainty in forest carbon budget projections. *Environmental Science and Policy*, **3**, 73–82.

Hese S, Lucht W, Schmullius C *et al.* (2005) Global biomass mapping for an improved understanding of the CO_2 balance – the Earth observation mission carbon-3D. *Remote Sensing of Environment*, **94**, 94–104.

Houghton RA (1999) The annual net flux of carbon to the atmosphere from changes in land use 1850–1990. *Tellus*, **51B**, 298–313.

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, Goodale CL (2004) Effects of land-use change on the carbon balance of terrestrial ecosystems. In: *Ecosystems and Land Use Change* (eds DeFries R., Asner G., Houghton R.A.), pp. 85–98. American Geophysical Union, Washington, DC.

Houghton RA, Hackler JL (1999) Emissions of carbon from forestry and land-use change in tropical Asia. *Global Change Biology*, **5**, 481–492.

Houghton RA, Hackler JL (2001) *Carbon Flux to the Atmosphere from Land-Use Changes: 1850 to 1990. ORNL/CDIAC-131, NDP-050/R1*. Carbon Dioxide Information Analysis Center, US Department of Energy, Oak Ridge National Laboratory, Oak Ridge, TN, USA.

Houghton RA, Hackler JL, Lawrence KT (1999) The US carbon budget: contributions from land-use change. *Science*, **285**, 574–578.

Houghton RA, Lawrence KT, Hackler JL *et al.* (2001) The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. *Global Change Biology*, **7**, 731–746.

Iverson LR, Brown S, Prasad A *et al.* (1994) Use of GIS for estimating potential and actual forest biomass for continental South and Southeast Asia. In: *Effects of Land Use Change on Atmospheric CO_2 Concentrations: South and Southeast Asia as a Case Study* (ed. Dale V.H.), pp. 67–116. Springer-Verlag, New York.

Laurance WF, Delamônica P, Laurance SG *et al.* (2000) Rainforest fragmentation kills big trees. *Nature*, **404**, 836.

Laurance WF, Laurance SG, Delamônica P (1998) Tropical forest fragmentation and greenhouse gas emissions. *Forest Ecology and Management*, **110**, 173–180.

Lefsky MA, Harding D, Cohen WB *et al.* (1999) Surface lidar remote sensing of basal area and biomass in deciduous forests of eastern Maryland, USA. *Remote Sensing of Environment*, **67**, 83–98.

Lucas R, Held AA, Phinn SR *et al.* (2004) Tropical forests. In: *Remote Sensing for Natural Resources and Environmental Monitoring. Manual of Remote Sensing*, **Vol. 4** (eds Ustin S *et al.*), John Wiley & Sons, Hoboken, NJ.

Matthews E (2001) *Understanding the FRA 2000*. Forest Briefing No. 1, World Resources Institute. Available on line at http://www.wri.org/forests/fra2000.html

Nemani RR, Keeling CD, Hashimoto H *et al.* (2003) Climate-driven increases in global terrestrial net primary production from 1982–1999. *Science*, **300**, 1560–1564.

Nepstad DC, Veríssimo A, Alencar A *et al.* (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, **398**, 505–508.

Olson JS, Watts JA, Allison LJ (1983) *Carbon in Live Vegetation of Major World Ecosystems. TR004*. US Department of Energy, Washington, DC.

Pacala SW, Hurtt GC, Baker D *et al.* (2001) Consistent land- and atmosphere-based US carbon sink estimates. *Science*, **292**, 2316–2320.

Patenaude G, Hill RA, Milne R *et al.* (2004) Quantifying forest above ground carbon content using lidar remote sensing. *Remote Sensing of Environment*, **93**, 368–380.

Phillips DL, Brown SL, Schroeder PE *et al.* (2000) Toward error analysis of large-scale forest carbon budgets. *Global Ecology and Biogeography*, **9**, 305–313.

Phillips OL, Malhi Y, Higuchi N *et al.* (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science*, **282**, 439–442.

Phillips OL, Malhi Y, Vinceti B *et al.* (2002) Changes in growth of tropical forests: evaluating potential biases. *Ecological Applications*, **12**, 576–587.

Plattner G-K, Joos F, Stocker TF (2002) Revision of the global carbon budget due to changing air–sea oxygen fluxes. *Global Biogeochemical Cycles*, **16**, 1096, doi: 10.1029/2001GB01746.

Rignot E, Salas WA, Skole DL (1997) Mapping deforestation and secondary growth in Rondonia, Brazil, using imaging radar and thematic mapper data. *Remote Sensing of Environment*, **59**, 167–179.

Schlesinger WH, Lichter J (2001) Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO_2. *Nature*, **411**, 466–469.

Steininger MK (1996) Tropical secondary forest regrowth in the Amazon: age, area and change estimation with Thematic Mapper data. *International Journal of Remote Sensing*, **17**, 9–27.

Treuhaft RN, Law BE, Asner GP (2004) Forest attributes from radar interferometric structure and its fusion with optical remote sensing. *BioScience*, **54**, 561–571.

Waring RH, Way J, Hunt ER *et al.* (1995) Imaging radar for ecosystem studies. *BioScience*, **45**, 715–723.